VOLUME XCIII NUMBER 2

THE

BOTANICAL GAZETTE

April 1932

ECOLOGY AND RELATIVE IMPORTANCE OF THE DOMINANTS OF TALL-GRASS PRAIRIE

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(WITH THIRTY FIGURES)

Introduction

This paper is the result of an intensive study of the vegetation of the prairie. The study extended over a period of ten years. It deals with the life histories, distribution, and relative importance of the dominant grasses in a central area of the tall-grass prairie. This area includes the grasslands of the western one-third of Iowa and those of approximately the eastern one-third of Nebraska. On the south it extends into Missouri and Kansas to the Kansas River. Northward it includes a small portion of southwestern Minnesota and a larger one of southeastern South Dakota.

Of the species concerned, all have been grown in experimental plots without competition; under various degrees of competition with other species; and in diverse natural habitats in the prairie. During the past three years 145 individual tracts of prairie have been carefully studied. In addition to the general surveys, hundreds of quadrats have been made in different types of upland and lowland prairies. The grassland areas ranged in size from 15 to 360 acres. They were selected so as to represent typical topography and also to secure rather uniform distribution throughout this vast area of over 60,000 square miles. None of the areas selected was grazed, disturbance being due only to late annual mowing. Just how far this

mowing has modified the original grasslands, which were both grazed and burned, cannot now be determined. But their resistance to invaders, even where the areas are entirely surrounded by them, shows in an impressive manner their high degree of stabilization and their wonderful adjustment to the environment.

Early in the study it was found that roadside observations are often entirely misleading in so far as giving an accurate picture of conditions prevailing in the prairie. Along roadways and in right-of-ways certain species make a good showing. Their conspicuousness and abundance are often such as to lead one to believe that they are really important in the prairie proper. Among such, the most common are *Stipa spartea*, *Elymus canadensis*, *Sporobolus longifolius*, and *Agropyron smithii*. In many cases these are found only sparingly, if at all, in the prairies, although occurring in considerable abundance where even a slight disturbance was made while building the road.

Among the various species of grasses in this centrally located area, the ten following were found to be the most important: *Andropogon furcatus*, *Sorghastrum nutans*, *Spartina michauxiana*, *Panicum virgatum*, and *Elymus canadensis* (all typical of relatively low lands); *Bouteloua racemosa* (of both moist and dry areas); and *Andropogon scoparius*, *Stipa spartea*, *Koeleria cristata*, and *Sporobolus heterolepis* (typical of uplands). It should be understood that upland and lowland are used only as relative terms to designate soils of lower and higher water content respectively. On large, nearly level, upland tracts, grasses demanding a continuously good water supply are found in the depressions. The water content of soil and other environmental factors of the prairie over a period of twelve years have been published elsewhere (**6**). Here only the development of the grasses based on these determinations will be given. Other herbaceous species will be treated in a subsequent study.

ANDROPOGON FURCATUS

Andropogon furcatus, big bluestem, is one of the two most important dominants of the prairie (fig. 1). Together with *A. scoparius* of uplands, it constitutes fully 70 per cent of the entire grassland cover. It is more mesic than the little bluestem and is best developed

on lower slopes and on well aerated lowlands. It does not thrive in soil that is frequently saturated. Under such conditions it gives way to *Spartina michauxiana*. Almost pure stands, except for a

FIG. 1 FIG. 2

FIGS. 1, 2.—Fig. 1, *Andropogon furcatus*, about 6 feet tall; fig. 2, *Sorghastrum nutans*

small admixture of *Poa pratensis*, *Sorghastrum nutans*, and a few non-grassy species, occur over extensive areas. A cover of 80–90 per cent of big bluestem is usual on well watered areas. On lower and mid-slopes it not only shares dominance with *A. scoparius*,

but also usually forms 5–25 per cent of the grassy cover on all but the driest hilltops and ridges.

The seedlings develop rapidly when conditions are favorable to growth. In the absence of competition, fine clumps, 12–18 inches tall, may develop in a single growing season and an occasional flower stalk be produced. Usually, however, this is accomplished in the prairie only after three or more years of growth. Winter-killing of the seedlings, and especially of the suppressed ones, is often severe; but after a second year of growth such losses are rather infrequent.

The primary roots develop rapidly. Two months after germination these range from 14 to 40 inches in depth.[1] Many of the roots of the secondary root system spread considerably, often 8–11 inches laterally at a depth of a foot. During the season, even under competition, the roots reach a working level of 2 feet or more. The very abundant roots of mature plants grow both vertically and obliquely downward. A few grow almost horizontally. They thoroughly occupy the soil and form a dense sod. Some roots may extend obliquely from the bunches more than a foot before turning downward. The mature roots are coarse (0.5–3 mm. in diameter) and, although better fitted for absorption than those of *Spartina*, are poorly branched in comparison with those of upland species. Depths of 5–7 feet are usually attained (**4**).

The tillering habit is pronounced. Seven or eight weeks after germination, tillers begin to appear and soon the seedling develops a small tuft or bunch. Rhizomes are also produced and the area occupied by both shoots and roots is thus greatly increased. The ability of this grass to compete successfully with other lowland species is in large measure due to its rapid development of tillers and rhizomes. Moreover it is very tolerant, especially in the seedling stage, where the leaves remain green and functioning under light values of 5–10 per cent. The lower leaves of plants, two or more years old, also make food under light values of only 10 per cent but only at about one-third the rate of fully lighted leaves.

[1] All data on growth, renewal of activity in spring, etc., are for the central part of the area. Growth in spring starts about seven days earlier on the southern border of the area and approximately ten days later on the northern one, thus making a total difference of more than two weeks.

As a result of the rhizome habit, this grass typically develops a characteristic sod. The individual stems are often spaced about 1 cm. apart. Even in the densest clumps they average less than one per square centimeter. Moreover, between these mats of sod there is much unoccupied soil. The total ground cover in this type rarely exceeds 25 per cent. Notwithstanding this open spacing, the foliage is so dense and the light so greatly reduced that invasion is extremely difficult. It is more or less successfully accomplished by *Poa pratensis*, and easily so owing to annual mowing.

Andropogon, being a genus of southern derivation, renews growth rather late in spring, usually not until the middle of April and several weeks after that of *Poa*. Bluegrass may blossom even before it is much shaded by its big competitor. *Poa* is found in the big bluestem type nearly 80 per cent of the time. It forms 1–15 per cent of the total ground cover. But on the upland, where the tall stems of big bluestem are often too few to reduce the light greatly, invasion is more readily accomplished. In contrast is the very dense sod of *A. scoparius*, where the area actually covered by the plants is rarely invaded.

Development of the shoots in the perennial sod is rapid. By the first of June there are three to five leaves and the average height is normally about 8–16 inches, varying with the habitat. By July 1, the level of the foliage reaches 12–18 inches on upland and 18–34 on low ground. By this time there are one to three dead basal leaves and four to seven large upper ones. The larger leaves have a width of 10–18 mm. and a length of 16 to more than 24 inches. They spread gracefully, so that the area of the top of a clump is usually 1.5 to twice that occupied by the base. The leaves have an osmotic pressure varying with the conditions of aridity of 7.4–14.5 A.[2]

The flower stalks begin to appear above the general level of the foliage early in July but anthesis does not reach its maximum until in August or September. The height attained by the flower stalks and the number of finger-like racemes produced vary greatly with the season and factors affecting growth, especially the water supply.

[2] Data on osmotic pressures of the various grasses were kindly furnished by Dr. H. WALTER, of the University of Heidelberg, who worked for a period during the spring and summer of 1930 in the botanical laboratories of the University of Nebraska (3).

On dry slopes flowering may not occur except during very favorable years, when flower stalks only 3 feet tall and with a single pair of racemes are not uncommon. But in the lowland both flower stalks and racemes are extremely abundant and well developed. For example, along the bottom lands of the Missouri River this rank grass reaches a height of 3 feet and the flower stalks 8–10 feet. The latter are woody, have a basal diameter of 5–8 mm., and possess nine to ten leaves. Fifteen or more terminal and axillary racemes are common on an individual stem. Over 200 such flower stalks frequently occur in a single square meter.

The seeds form from late in August until frost. Each is provided with a long, bent, and twisted awn. During late September the foliage begins to dry. The plant then develops the beautiful tints of red and brown or bronze so characteristic of the autumnal landscape.

Big bluestem is an excellent grass to pasture, and also furnishes one of the chief constituents of the "wild" or "prairie hay." It is highly valued as a hay, but must be cut in early bloom or stock will reject it since the stems become too hard and fibrous. On lowlands, where it is best developed, usually two cuttings are made each summer. The new growth rapidly develops and furnishes an abundant second crop.

SORGHASTRUM NUTANS

Sorghastrum nutans, Indian grass, is a tall, coarse species with a water requirement and habit almost identical with those of *Andropogon furcatus* (fig. 2). It is, however, of much less importance. It occurs in greatest abundance in Kansas and southward, but like *Panicum virgatum* it accompanies *Elymus* through the great valleys like the Platte although it is regularly to be found most abundantly in the moister levels. Here it forms clumps of pure sod from a few inches to a few feet in diameter, or, more often, is intermixed with the other lowland species, especially *Andropogon furcatus*. It may constitute 90 per cent of the vegetation where almost pure areas occur in ravines, etc., but this falls to only 5–20 per cent where it is best developed in lowland mixtures. The more usual percentages, however, are 1 to 5 and in many lowlands it is almost absent. Its occurrence in dense, big bluestem sod as isolated stems or very small

clumps is usual. It can easily be distinguished from the latter, which it most closely resembles, by its slightly more erect habit of growth, usually broader leaves, slightly lighter green color, and especially by the very prominent ligules. Where lowlands are occasionally flooded or otherwise disturbed, *Sorghastrum nutans* greatly increases in abundance.

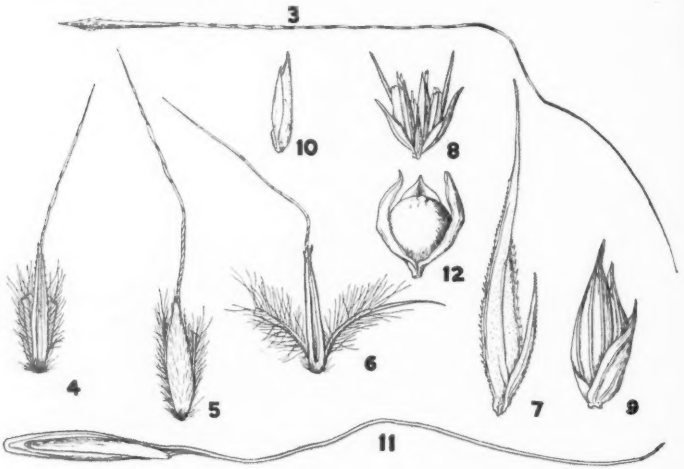
This grass accompanies *Panicum virgatum* and *Andropogon furcatus* up the moist slopes and ravines and is found widely scattered over the broad drainage areas which conduct run-off water. Even on high crests and ridges it may constitute locally 5–25 per cent of the vegetation. Southward it often ranks closely to *A. furcatus* in its importance in upland. Northward it is usually much less abundant and is often almost absent.

The rather large seeds are usually viable and germinate readily unless buried more than half an inch. The seedlings are vigorous and endure a wider range of extremes as regards drought than most lowland species. This probably explains, in part, the habit of this species of readily invading disturbed areas throughout the prairie.

Seedlings develop with marked rapidity, reaching a height of 8–12 inches in three months. Under severe competition, tillering is practically nil, a fact that accounts for the occurrence of single stems of this grass scattered among other species. Where there is little competition three or four tillers and a few short rhizomes are usually to be found by August. Thus single seedlings may soon develop into a small tuft or bunch, or fuse with others into a larger mat of sod. The roots of such seedlings spread widely in all directions to the extent of a foot or more at the 12-inch level. This spreading habit is significant in the competition of seedlings for water in the surface soil. A working level of 18 inches and a maximum penetration of 12–16 inches usually result in an abundant supply of water.

The mature root system reaches a depth of 4–5 feet, which is somewhat less extensive than that of several of the other dominants. However, it is more finely and abundantly branched; hence the plant often succeeds in colonizing dry habitats. Ordinarily a second and sometimes a third season is required for the production of flower stalks, but in moist soil and without competition the life cycle is completed in a single year.

Being of southern derivation this grass begins growth late in spring and ripens its seeds late in autumn. Like big bluestem, it often does not renew growth until after the middle of April, but development is rapid. Within a month the plants may be 10 inches tall and more than twice this height by the first of July. Under favorable conditions the foliage (exclusive of flower stalks) may attain a height of 3.5 feet but it is usually about 2.5–3 feet. The leaves are 8–18 mm. broad and the blades are usually 1–2.5 feet in



FIGS. 3–12.—Fig. 3, fruit of *Stipa spartea*, ×¾; fig. 4, spikelet of *Andropogon furcatus*, ×2.5; fig. 5, spikelet of *Sorghastrum nutans*, ×2.5; fig. 6, spikelet of *A. scoparius*, ×2.5; fig. 7, spikelet of *Spartina michauxiana*, ×2.5; fig. 8, spikelet of *Bouteloua racemosa*, ×2.5; fig. 9, spikelet of *Panicum virgatum*, ×5; fig. 10, floret of *Koeleria cristata*, ×5; fig. 11, floret of *Elymus canadensis*, ×2.5; fig. 12, fruit of *Sporobolus heterolepis* with attached scales, ×5. All are shown just as they fall from the parent plant.

length. By early summer one or two of the lower leaves are dead and the four or five remaining ones clothe the stem, which is green to the base. The osmotic pressure was found to vary between 8.6 and 11.7 A.

The stems are coarse (3–6 mm. in basal diameter), and even in good stands they average only 4–7 (but sometimes 11–15) per sq. dm. Since there are practically no living basal leaves, more than

90 per cent of the soil surface may be unoccupied; but generally there is a sparse understory of bluegrass and very tolerant forbs. The spread of the tops usually only slightly exceeds twice that of the area occupied by the base, since this species grows rather erect.

Flower stalks begin to appear late in July, and anthesis reaches its height late in August and in September. The large panicles are 4–12 inches long. Since the paniculate inflorescence stands well above the foliage, a total height of 6 to over 9 feet is attained. The seeds, which are disseminated from late in August until winter, are furnished with a bent and twisted awn which is about four times the length of the seed (fig. 5). During September and October the drying leaves give the various shades of yellowish and reddish brown that make the grass conspicuous throughout the winter.

Like big bluestem, this species is an excellent one for grazing and for hay. If cut before the woody flower stalks develop, it is readily eaten by all kinds of stock.

Spartina michauxiana

Spartina michauxiana, tall marsh grass or slough grass, is really not a dominant of low prairie but is the final consocies of the hydrosere leading to the prairie proper (fig. 13). This conclusion is drawn from its successional behavior in the field and from an experimental study of *Spartina* in competition with *Andropogon furcatus* (1, 2). It grows typically in the edge of sluggish streams or ponds and in water-logged or wet soil, rarely occurring in moist soils except in dry seasons or as relicts in soils that have been drained. Its demarcation of soils too wet and consequently too poorly aerated for the growth of maize is clearly shown throughout the prairie. In countless areas the uplands and big bluestem lowlands have been broken, but the slough grass draws and flooded lands were left intact. They are too wet for cropping, at least in spring, but furnish excellent hay, and very successfully hold the soil against erosion. Vast areas of "first bottom" along the Missouri River and its tributaries are covered with *Spartina*, often in almost pure stands. Toward the mesic side it gives way to *Andropogon furcatus*, usually through a transitional zone characterized by *Panicum virgatum* and *Elymus canadensis*. More hydric species of tall sedges, rushes, etc.,

such as *Carex vulpinoidea*, *C. hystricina*, *Scirpus atrovirens*, etc., mark the transition to the earlier reed-swamp stage.

The seeds germinate readily in wet soil, and within a month the seedlings are 2–4 inches high and have developed three or four leaves.

FIG. 13 FIG. 14

FIGS. 13, 14.—Fig. 13, *Spartina michauxiana*, 6.5 feet tall; fig. 14, *Panicum virgatum* in full bloom, about 5 feet high.

Early in August, even in moderately moist soil, an average height of 12 inches is attained, and by the end of the first summer this is increased to 2.5 feet. The seedlings are not very tolerant of shade.

The lower leaves of suppressed plants die and the upper ones are greatly attenuated; finally the whole plant succumbs. The dominants ordinarily require two or more years' growth before flower stalks are produced. By this time the mature foliage is 3–5 feet high and the photosynthetic surface very great. Because of its tall growth in dense, pure consocies, light values near the soil surface are only 1–3 per cent. Reproduction except in bare areas is undoubtedly almost entirely vegetative.

The rapid development of shoots is paralleled by that of the underground parts. The primary root system elongates at an average rate of nearly 0.5 inch per day, and early in August may reach the 3-foot level. By this time several rhizomes, 2–5 inches long, have developed as well as a good secondary root system. Unlike many upland species, the roots grow almost vertically downward from the plant and its rhizomes and have practically no lateral spread.

Beneath mature plants the surface 6–10 inches of soil is filled with a mat of coarse, woody, very much branched rhizomes, 5–8 mm. in diameter. They vary greatly in length, extending outward 2–15 inches before giving rise to erect shoots. They are covered with long, overlapping leaf scales; the younger ones, especially, are tipped with long, sharp-pointed buds, an adaptation for penetrating heavy, compact soil. The depth of root penetration is surprising, considering the water relations of the habitat. Depths of 8–10 feet are commonly found in wet soil. The coarse, tough roots are 3–5 mm. in diameter and only moderately well branched. In fact, this grass has coarser roots than any of those of the prairie proper (**5**). When grown in drier soil, branching becomes much more profuse. Blocks of *Spartina* sod when transplanted to high upland developed profusely branched roots 11 feet long and persisted, producing short flower stalks on wet years, for a period of ten years.

Although this species renews activity rather late, often not until the second week in April, it grows more rapidly than any of the grasses of the prairie. By the first of June it is frequently in the fifth- or sixth-leaf stage and varies from 2 to over 3 feet in height. Where it shares marginal areas with *Panicum virgatum* or *Andropogon furcatus*, it conspicuously overtops them. The general height of

the leaves at the end of the growing season varies from 3 to 7 feet, depending upon the water supply. Because of the extensive rhizomes this species always forms a sod. Where best developed, the coarse woody stems, which are 2–10 mm. in diameter, are widely spaced. In the densest cover there is usually only one stem for every 3–20 sq. cm. of soil surface, and the surface actually occupied is often only 1–3 per cent.

Where an abundant and constant water supply favors the growth of *Spartina*, other grasses are effectually excluded. Although often in groups of three or more, the stems are more usually singly spaced and the cover is uniform. The shade is dense. Two or three of the basal leaves are generally dead by midsummer, leaving the stems bare to a height of about 8–12 inches. The six or seven living leaves, where water is plentiful, are sometimes 15–18 mm. in width and 2.5–5.5 feet in length. The osmotic pressure of the leaves varied from 11.4 A. in early summer to 16.4 during a September drought. These determinations, however, were made on relict plants in low prairie.

Even in moist soil the flower stalks are 5–6 feet tall and in wet areas often reach 9–10 feet. Flowering begins about the second week in July, but the height of anthesis occurs approximately a month later. Flowering may continue until frost. The large, conspicuous panicles are 12–24 inches long and 6–10 inches wide.

Slough grass makes good hay if it is cut before the woody stems are much developed. The common practice is to mow the sloughs about three times each year. Since growth is quickly renewed and very rapid, heavy yields are thus assured. Slough grass is also used for thatching sheds and covering hay stacks.

PANICUM VIRGATUM

Panicum virgatum, tall panic grass, a tall, coarse, rank, sod-forming grass, is an important dominant of low, moist soil (fig. 14). It has migrated far up ravines and draws and also occurs in disturbed areas in uplands. It is more important in the southern and eastern portions of the area where the climate is more humid as well as warmer. It is perhaps the most mesic of prairie grasses, as is shown by its abundance in the drier portions of the *Spartina* consocies, occupying with *Elymus canadensis*, *Agrostis alba*, etc., areas that

are too poorly aerated for the big bluestem. It is rarely found in extensive pure stands, the clumps and areas usually alternating with *Spartina, Carex vulpinoidea*, etc. In such mixtures it covers many square miles of poorly drained bottomlands along the Missouri and its tributaries, constituting 10–30 or more per cent of the vegetation.

Tall panic grass is almost invariably found as a transitional species along ravines and draws wherever big bluestem gives way to *Spartina michauxiana* (or southward to *Tripsacum dactyloides*). The transition, whether gradual or abrupt, is characterized by small patches of dense pure stands, by clumps often 3–4 feet in diameter, and by an intermingling with the bluestem on its marginal areas. While *Panicum* may locally constitute 25 per cent of the grass mixture, this often falls to 10 per cent, and, where big bluestem is well developed, to less than 3 per cent.

Panicum is found in areas of higher water content along draws and the broad sloping flats receiving run-off water at the heads of draws. The rank growth at the bottom of ravines, where it is often 5 feet high, gradually decreases to about 3 feet near the top. Moreover the exclusive, dense sod becomes thinner as the grass extends its area into drier lands, often a rod or two on the sides of the draw, until only scattered, dwarfed individual stems one to several inches apart occur. On the uplands it secures a foothold in areas of greater water content, where disturbance has occurred. Here it is found widely scattered in small clumps or as isolated individuals, and is of no importance in the percentage composition of the cover of vegetation.

Seeds of this species usually give a low rate of germination and propagation is undoubtedly largely by rhizomes. The seedlings develop rapidly. Unless competition is too severe, tillering and rhizome production begin in five to seven weeks. Where the light is reduced to 5–10 per cent, near the soil surface, suppressed plants make food at only one-half the rate of dominant seedlings. This species appears to be less tolerant than big bluestem. Seedlings persist for two years, however, in disturbed areas occupied by dense growths of coarse herbs, such as *Oenothera biennis*, under a light intensity of 12–20 per cent, and take complete possession of the area upon the disappearance of the herbs.

Three months after germination, heights of 12–20 inches are attained. By this time a typical seedling possesses two or three tillers, two to four rhizomes, some half an inch in length, and a good root system 12–30 inches deep. This species, however, does not tiller as readily or as abundantly as big bluestem, and in addition the mortality of seedlings due to winter-killing is often very great.

Unlike the vertical roots of *Spartina*, those of *Panicum* spread 5–6 inches in all directions when only 6 inches deep. The roots are extensive but very coarse, and lack the profuse network of branches characteristic of upland grasses (fig. 15). They may attain a depth

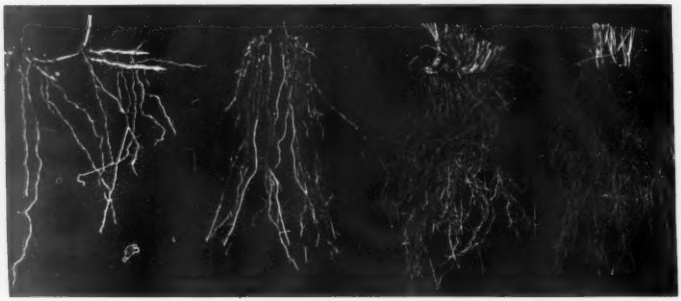


FIG. 15.—Portions of root systems of *Panicum virgatum* (left), *Andropogon furcatus*, *A. scoparius*, and *Koeleria cristata* (right), showing the much finer roots of the two upland species.

of 5 feet in a single summer. Under favorable conditions the root system may more than double in length during the second season, the foliage reach a height of 3 or more feet, and flower stalks be produced.

The mature root system is the longest of any of the grasses of the prairie. The roots are very coarse, many being 3 or 4 mm. in diameter. They pursue a vertically downward direction, spreading only a little near the surface, to a maximum depth of more than 9 feet.

Since this species is of tropical derivation it renews growth late in spring, often about April 20. Owing to an abundant food supply in roots and rhizomes, it grows rapidly, and by June 1 is 18 inches high and in the third- or fourth-leaf stage. It is always distinctly taller than the big bluestem. Where mowing or fire does not remove it, the accumulated débris is often 7–10 inches thick the following

spring. This receives the insolation rather than the soil and results in a colder habitat which delays growth. After two years' accumulations such a cover is decidedly harmful and tends to reduce the stand.

The height attained by mature plants varies greatly with season and water content. On uplands it is often 3–3.5 feet; in wet lowlands a maximum height of 4.5–6 feet is attained. Fully developed plants in close stands usually have one to three dead basal leaves and six or seven living ones, all on the coarse, woody stems which are 2–5 mm. thick. The flat leaves are 14–24 inches long and 8–14 mm. wide, thus presenting a large photosynthetic surface. They reduce the area by rolling during dry weather. An osmotic pressure of 13.7 A. has been determined for this species during a period of drought. As with the preceding grasses, nearly full height of the vegetation is attained by the middle of July. Then large, open, spreading panicles, which become 12–20 inches long and 16–20 inches wide, begin to appear. Flowering begins in July, reaches a maximum in August, and continues until frost in late September or October. The seeds are shed in late fall and winter.

Owing to the lack of basal shoots and the wide spacing between the unbranched stems, only a small amount of the surface soil is actually occupied. In good stands only 4 to 24 stems occur per sq. dm. and 90–95 per cent of the ground is bare. *Poa pratensis* and various carices often occur as interstitial species, but usually sparingly because of the low light intensity. Their roots absorb from the soil occupied by the dense mats of coarse rhizomes and roots of the tall grasses. In regard to the light relation also, *Panicum* has much the advantage.

This grass affords good grazing when young, but as the stems become lignified forage value greatly decreases. Stock, however, eat the panicles and leaves even of mature plants. It is excellent for hay, and when cut before the stems become woody (usually twice per summer) it gives large yields.

Elymus canadensis

Elymus canadensis, nodding wild rye, is also a tall, coarse grass of high water requirement (fig. 16). Although of wide and regular distribution, over the prairie as a whole it is a dominant of minor

importance. It is typically a lowland species, reaching its best development in the wet transitional areas between *Spartina michauxiana* and *Andropogon furcatus*. It also intermingles more or less with both of these. On uplands it is found usually only where local disturb-

FIG. 16 FIG. 17

FIGS. 16, 17.—Fig. 16, characteristic clump of *Elymus canadensis*, about 5.5 feet high; fig. 17, large clump of *Bouteloua racemosa*. Flower stalks about 3 feet tall.

ances, such as gopher mounds, badger holes, etc., have occurred. With *Panicum virgatum* it forms a reliable indicator on upper slopes and ridges of increased water content due to local denudation. Once in possession the bunches or clumps may remain for many years.

The persistence of a species when once established is worth careful consideration. Possession by long-lived species is the law in grassland. For example, clumps of *Elymus*, *Panicum*, and *Spartina* transplanted to the crest of a dry hill among upland grasses, such as *Stipa*, *Koeleria*, etc., have persisted, some for ten years. They have rooted deeply, *Panicum* and *Spartina* to 11 feet. Although unable to extend their areas, during wet years they put forth flower stalks and blossom.

Elymus occurs only in isolated clumps in uplands, and even on lowlands it forms pure stands only in very local areas. Usually it constitutes a 1–5 per cent mixture among the other grasses and exceptionally 10–15 per cent. Northward and westward it becomes more abundant than in the south and east. On level land subject to overflow, and too wet for big bluestem, it often covers large tracts resembling thinly planted fields of barley. Examination shows that the abundance is more apparent than real. Rarely more than 40 to 50 stalks occur per square meter. Since during midsummer there are few or no basal shoots or leaves, this grass may form only 5–8 per cent of the ground cover.

The relatively large seeds show a high rate of germination as determined by experiments extending over a period of ten years. Unlike most grasses, even when the seeds are covered with soil to a depth of 1–2 inches they still produce seedlings abundantly. Within a month the plants are 2–3 inches tall and in the third-leaf stage. Early in August a height of 6–10 inches is attained. Where grown without competition (as in locally denuded areas) it often exceeds a foot in height, and sometimes produces small flower stalks the first season. Flower stalks are developed the second year even under close competition. Because of its northern derivation, seedlings do not badly winter-kill.

Development of the underground parts also takes place rapidly. After three months' growth, the well developed and widely spreading roots reach a working level of 18 inches and a depth of 25–30 inches. Although the primary laterals seldom exceed 2 inches in length, they are branched to the third and fourth degree.

Tillering begins early, only four or five weeks after germination. By midsummer all but suppressed seedlings have one to three tillers

each. The short rhizomes result in the formation of bunches or clumps.

The roots of mature plants seldom exceed 2.5 feet in depth and are thus much shallower than other lowland dominants. The obliquely running roots may spread nearly 2 feet on all sides of the plant, however, and the roots are more finely branched than those of the other lowland dominants, with the possible exception of *Sorghastrum nutans*.

Growth is resumed very early in spring. Late in March new shoots are frequently 3–5 inches long and bear several green leaves. This takes place before *Panicum virgatum*, *Sorghastrum nutans*, and other tall-grass competitors have renewed growth, giving *Elymus* a great advantage in competition, especially for light.

Elymus reaches a height of 30–40 inches by the middle of June, and soon the spikes begin to appear. These are 6–9 inches long and often 1 inch in diameter, including the awns. The stout, rather woody stems are 3–5 mm. thick. They usually occur in loose clumps or are widely spaced in a more or less continuous, open sod. They usually have one or more withered leaves and seven to eight green ones. The flat leaves are 10–20 mm. wide but only 8–15 inches long. The osmotic concentration of the cell sap of the leaves ranged from 13.0 A. in spring to 19.1 A. during severe drought. A period of maximum blooming occurs during July. During the ripening of the seeds the spikes bend over gracefully, which accounts for the very appropriate name, nodding wild rye.

Elymus is a good forage grass, and when cut early furnishes an excellent component of "prairie hay." If mowed late the stems are woody and the heads are often infested with ergot.

BOUTELOUA RACEMOSA

Bouteloua racemosa, side-oat grama, is scattered widely throughout the prairie in all types of situations, but rarely occurs in great abundance. The largest undisturbed area found that was controlled by this tall grass did not exceed a few square meters. It nearly always occurs as small, isolated, rather open tufts scattered among the other species, especially in the *Andropogon furcatus* type of prairie (fig. 17). A 1–3 per cent mixture is common, even on uplands, and

it may occur as abundantly as 10 per cent locally. Its habit approaches that of an interstitial species, and where there is disturbance, such as is caused by erosion on steep banks, etc., it frequently increases in abundance. Quadrats in old roads along ridges sometimes give an abundance ranging from 15 to 60 per cent. It withstands grazing rather well and increases in territory under moderate pasturing. Although nearly always represented in any considerable area, its importance is not great.

The seeds are usually viable and give a good rate of germination even when buried an inch in the soil. The seedlings make an excellent growth and tiller vigorously. In a bare area, for example, the seedlings were 11 inches tall by July 30, when the roots had reached a working level of 18 inches and a maximum depth of about 3 feet. The plants bore seven or eight tillers, fifteen roots, and one or two rhizomes. Even at a foot in depth the laterals were sometimes 9 inches long, and spread widely through the upper levels of the soil. By October, flower stalks 1.5 feet tall were abundant and a large crop of seed was produced. Under competition, however, rate of growth is much reduced and blossoming ordinarily does not occur until the second or third summer.

Its tall stature and excellent absorbing system, together with its tolerance of shade, enable this species to compete more or less successfully for a place in the sod.

This *Bouteloua* renews growth late in April at about the same time as the bluestems. It grows rapidly, reaching a height of 3–3.5 feet and a depth of 5–6 feet. Tillers arise abundantly from the numerous short rhizomes and the spreading base of the plant is well clothed with rather short leaves. The unbranched stems have five to seven leaves each, which are progressively shorter from the second one to the top. The leaves vary in length from 4 to 14 or more inches and are about 5–7 mm. wide. An osmotic pressure of 12.6 A. has been found during midsummer. The dry, curled, whitish, rather hairy basal leaves are characteristic and readily mark this species in the vegetative state.

Flower stalks begin to appear about the first week in July and anthesis continues through August and September. The racemes are 6–12 inches long and have anywhere from 25 to 50 spikes, all usually

hanging gracefully from one side. Even when all the spikelets have fallen, the species is readily identified by the zigzag rachis.

This grass furnishes nutritious forage for all kinds of stock, and is readily eaten at all times, even in the dormant condition. It furnishes a minor constituent of the hay from the prairie.

FIG. 18.—Characteristic bunches of *Andropogon scoparius*, showing leaves about 15 inches tall and mature flower stalks.

ANDROPOGON SCOPARIUS

Just as *Andropogon furcatus* is the most important dominant of low prairies, so also *Andropogon scoparius*, little bluestem, forms the great bulk of the upland grass cover (fig. 18). It easily exceeds

in importance all of the other upland species combined. In the south and east, where moisture is more plentiful, its chief competitor is big bluestem. In the north and west, especially on poor soils and areas with extreme run-off, it is intermingled with *Stipa spartea*, which sometimes replaces it in local areas.

This species ordinarily forms a much interrupted sod, best developed northward, in which the mats or tufts are so dense that few other species can invade them. Accompanying species grow between the mats or bunches. Where the slopes are steep and the run-off and erosion are great the bunch habit becomes pronounced.

On the deep soils of the steep, drier, loess hills, this species alone frequently constitutes 90 per cent of the vegetation, and in drier soils as a whole, including level uplands, 50 to 75 per cent. On midslopes and lower hillsides it forms alternes or more usually intermingles with the big bluestem, often on equal terms. On lower lands the big bluestem and other taller grasses have the decided advantage in securing light, and if there is sufficient water for a continuous cover of the taller grasses, little bluestem entirely disappears.

The percentage of germination is often low but the seedlings are vigorous. During the first summer they reach a height of 6–8 inches and tiller profusely. For example, seedlings in late July were 5.5 inches tall. They had developed three or four tillers and eight roots each. The latter reached a working level of 12 inches and a maximum depth of 18 inches. The young roots are fine and extremely well branched, some of the branches attaining lengths of 3–4 inches. Thus the plant is well fitted to absorb in relatively dry soil. In the absence of competition it may complete its life cycle by producing flower stalks and seeds the first year; but in the prairie, this requires two seasons very favorable to growth, and ordinarily three or more. The mature root system consists of a vast network of threadlike roots and masses of finely branched rootlets, some over 30 inches long. Thus the soil beneath the sod and several inches on all sides of it is filled with a dense mat of roots to a depth of about 5 feet. Such an absorbing system is remarkably efficient.

The leafy stems grow compactly in the sod mat. Even where poorly developed, 50–80 stems occur per sq. dm. and there are often 100–300 crowded into a similar area. Many of these are furnished

with several tillers each and all are leafy to the base. Thus the mat is compact and there is little room for invasion. The density of the mat varies with the water relation and also with age. On lower slopes and in areas of greater rainfall the whole sod may consist of closely crowded stems, but on uplands during dry years the center may have few stems and the peripheral ones show a markedly better growth. Deterioration of the clump nearly always occurs first in the older, central part and proceeds toward the periphery. The leaves are usually only 3–4 mm. in width and 4–8 inches long, but sometimes measure as much as 18 inches. Usually only the three or four uppermost ones are green and one to three dried, dead ones clothe the base of the stem. Where the grass is not mowed, the dead leaves intermingle with the living ones to a height of about 7 inches. An osmotic pressure of 7.9–30.4 A. has been determined for the foliage.

The size of the sod mats is variable. In favorable situations solid clumps 1.5 by 2 feet in extent may be found; but normally they are smaller, often 6–8 inches or less, and rather irregular in shape. Often the sod consists of smaller tufts rather closely aggregated, so that the overlapping leaves give an apparent cover of 80–100 per cent; actually the basal cover in any case seldom exceeds 25 per cent. Larger and better filled clumps occur southward, while the best development of the tufted sod-mat type is frequently found in northern Nebraska and Dakota. When the foliage is well developed, the spread of tops is often approximately twice that of the basal area. The height attained by this species is variable. It ranges from 7 to 10 inches on dry hilltops and regions of lowest rainfall to 20 inches in the warmer, more humid regions southeastward. On moderately low lands, in competition with the taller grasses, the leaves attain heights of 2–3.5 feet.

Growth begins in late spring, often about April 15, and at a time when *Stipa spartea* and *Koeleria cristata* have well developed bunches. Flower stalks begin to appear by the middle of July and are abundant late in August. The inflorescence consists of a single raceme from each peduncle. These are terminal both from the main stalk and its branches. The raceme is loose and usually 1–2.5 inches long. The flower stalks vary from 1.5 to 2 feet high on dry uplands,

where blossoming may occur only in exceptionally wet years, to 3–4 feet under a more favorable water supply. Flower stalks are usually thickly grouped and seeds are produced in great abundance. Each has a twisted awn about 0.5 inch in length (fig. 6). By early winter nearly all the seeds have been dislodged by the wind, but the old flower stalks persist for a long time. The beautiful autumnal coloration of upland prairie is largely due to the various shades of yellows, reds, and bronze afforded by the drying plants of this species.

Little bluestem is a rather good forage grass and furnishes satisfactory grazing when the dry stems do not interfere. It is a chief constituent of hay from upland prairie, and is best when cut early.

Stipa spartea

Stipa spartea, needle grass, is typically an upland species (fig. 19). It is practically of no importance in the portion of the area in Kansas and Missouri, but gradually increases in abundance and is an important species of the prairie northward. Steep, dry ridges and xeric slopes, especially where the soil is thin and perhaps sandy or gravelly, are frequently more or less dominated by *Stipa*. Such areas alternate with *Andropogon scoparius* or *Sporobolus heterolepis* (to be described), or even with a more or less equal mixture of the bluestems. Its chief associates are *Koeleria cristata* and little bluestem, but it is found in various grassy mixtures.

Because of its excellent growth on dry banks along roadsides and its very deceptive appearance as regards abundance, its frequency and importance are easily overestimated. Even where the bunches are a foot apart, the widely spreading leaves and gracefully bending stems, which may extend 1–3 feet on all sides of the clump, give the appearance of a thick growth. A study of the composition of the vegetation in which *Stipa* appears to dominate shows that it often constitutes only 15–35 per cent of the prairie. Rarely does it comprise 50–80 per cent of the plant cover and this only in local areas. In many prairies it is scarcely represented; usually it forms 1–5 per cent of the vegetation as a whole; but in hilly lands in the central and northern parts of the area alternes of *Stipa* may cover from one-fifth to one-third or even more of extensive uplands. Moreover, it is

frequently more or less abundant on flat lands at the heads of draws, and is readily distributed over broad washes on lower slopes that are subject to overflow and deposit during exceptionally heavy rains. Here it is found with big bluestem, usually in no great abundance, but sometimes dominating rather extensive local areas.

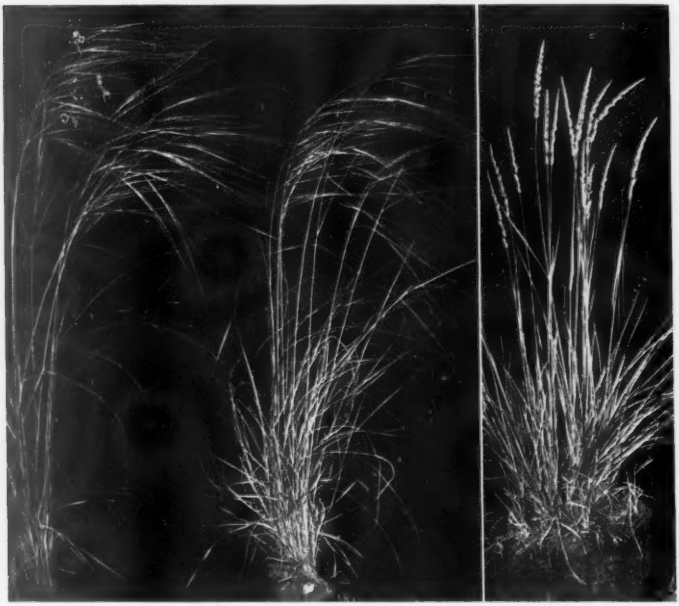


FIG. 19 FIG. 20

FIGS. 19, 20.—Fig. 19, bunches of *Stipa spartea* with fruits maturing, height about 3 feet; fig. 20, *Koeleria cristata*, just after blooming, flower stalks 2 feet high. (Photographed June 15, 1931.)

The large, heavy seed in the long-awned fruit germinates usually only after being worked 1–3 inches into the soil. The seedlings make a good growth and by midsummer the parent culms are often 8–12 inches tall and possess five leaves and three or four tillers. By this time the fine, well branched root system is usually 15–20 inches deep and in good contact with the moist subsoil. True to its boreal extraction, year-old *Stipa* seedlings begin growth in March. They are

4–6 inches tall and are in the third- or fourth-leaf stage before most other grasses have broken their dormancy. By the second summer the foliage may reach a height of 2 feet, but flower-stalk production ordinarily does not occur until the third year. The root system of even mature plants seldom reaches a depth greater than 2.5–3 feet, but it is exceedingly well fitted for absorption in the upper soil levels. Numerous, profusely branched, smaller roots fill this region, and the larger ones give rise to many laterals which divide into fine branches in the deeper soil.

The production of tillers and short rhizomes gives rise to more or less circular clumps or bunches; this species never forms a sod. The size of the clumps is variable depending upon conditions of growth; some are only 1 cm. in diameter, the largest perhaps 12 by 12 cm. A very usual size under ordinary conditions is 3 by 5 cm. The bases of long, spreading clusters of rosette-like leaves remain partly green during the winter, although the distal two-thirds' portions of the leaves are usually frozen. Growth begins with the first warm days and the foliage is often 2 feet high by the first of June. At this time flower stalks are well developed.

The flower stalks are from 2 to 4 feet tall. Tufts 1 or 2 cm. in diameter may have only one or two flower stalks, but large clumps in more favorable areas may produce 18 or more. During dry springs seed production is greatly reduced.

The height of the foliage varies from 14 to 36 inches, depending upon the degree of competition and the amount of available water. The somewhat glaucous, rather stiff, deeply ridged leaves are only 3–4 mm. wide but 1.5–3 feet or more long. The long attenuated ends are mostly dead and dry. There are usually only three living cauline leaves and one or two dead ones. The ligules are prominent. An osmotic pressure of cell sap of 12.7–24.4 A. has been determined.

By June 10 the twisting awns, which are 4–6 inches long, indicate the ripening of the seed. Usually by the first week in July the seeds have all fallen and are widely scattered by the wind. The fruit is buried in the soil by the torsion of the bent and twisted awn, which is held from turning by the bases of the grass stems. This excellent method of planting the seed compensates for the small number, which ordinarily ranges from 12 to 25 for each robust flower

stalk. Even after the seeds have fallen, the persistent, broad, drying scales (3–4 cm. long) on the spikelets glisten in the sun so that the whole hillside, where the plant is at all abundant, has a silvery appearance.

Wherever *Stipa* is thick, the ground cover is very open, and the greater the apparent density of the species the barer the soil. For example, in quadrats with 25–35 bunches of moderate size only 5–7 per cent of the surface soil was occupied. Where the number drops to 8 or less per sq. m. other grasses occur more abundantly and the total cover correspondingly increases. These relations hold on even relatively low land.

In general, *Stipa*, with *Koeleria cristata* and *Sporobolus heterolepis*, occurs on more immature soils and thus represents an earlier stage in development than do the species of *Andropogon*. The ability of *Stipa*, especially, to colonize thin soils and disturbed areas is due partly to its excellent method of deeply planting the seeds in contact with moist soil; partly to its excellent and rapidly developed root system; and partly to its early growth, by means of which it avoids excessive competition. The last, however, is detrimental under grazing and explains why *Stipa* is among the first grasses to disappear. Animals feed on it at a time when the other upland grasses have commenced little or no growth. Such grazing greatly decreases growth, limits seed production, and may result in the disappearance of the species.

KOELERIA CRISTATA

Koeleria cristata, June grass, is a bunch grass but of smaller stature than any of the preceding (fig. 20). Like *Stipa*, it is of boreal origin and is abundant in the northern part of the area. It shows a decided preference for dry uplands and is typically associated with *Stipa spartea*, *Sporobolus heterolepis*, and *Andropogon scoparius*. Not infrequently, however, it occurs also on lower mid-slopes as well as on well drained lowlands.

The necessity of good aeration for upland species and the greater tolerance of those of lowland to deficient soil air resulting from high water content are well illustrated in the following experiment.

Late in April large blocks of sod were removed to a depth of about 8 inches and transplanted into a *Spartina* swamp. These

blocks contained all of the more important prairie species and also included *Spartina michauxiana*. The last was dug up and replanted in its native habitat. The soil was completely saturated until about June 15 and a high water content prevailed throughout the summer.

By the first of June *Andropogon scoparius* died; most of the leaves were dead on *Koeleria;* and all of the upland species, especially, showed by wilting and dead leaves the harmful effect of deficient aeration. The middle of June found *Bouteloua racemosa* dead; *Stipa* had almost succumbed; the flower stalks of *Koeleria* had rotted to the base, and only a few green leaves remained. A month later both *Koeleria* and *Stipa* had died, thus completing the mortality of upland species.

The species native to low prairie did much better, although those requiring the most aeration (*Andropogon furcatus* and *Sorghastrum nutans*) died by the end of summer. *Elymus canadensis* lost most of its leaves and the flower stalks completely decayed at the ground line, but it sent forth new basal shoots. *Panicum virgatum* and *Spartina* grew very well, the latter flowering in a normal way. The swamp was somewhat drier the following year and all three of these lowland species became firmly established.

In many prairies, especially southward, *Koeleria* may be scarcely if at all represented; but it more usually forms 1–3 per cent of the cover, at least locally. An abundance greater than 5–10 per cent has rarely been found except in disturbed places. The small tufts are widely distributed, however, and upon close inspection isolated plants may frequently be seen.

The seeds are produced in great abundance and usually give an excellent germination. The seedlings have much more difficulty in becoming established than those of most prairie grasses. During summer drought the mortality is always high and many are also winter-killed.

The dominant seedlings tiller freely and soon a small clump is formed, the plants often reaching 3–8 inches in height the first season. Usually two or three years are required for the production of flower stalks.

The root system is relatively shallow (15–28 inches) but fine and exceedingly well developed. A great network of fine rootlets spreads

outward from the base and occupies the soil to a distance of 8 inches on all sides of the plant, some absorbing within 0.5 inch of the soil surface. It may be, as in the case of *Stipa*, that the early growth in spring and rapid maturity of this species are correlated with the shallow root system.

Koeleria makes an excellent growth after the fall rains and remains green after most of the grasses have dried. With the first days of spring, growth is renewed vigorously and then the green clumps are conspicuous against the background of dead foliage. By the end of May the foliage is often 12–15 inches tall and flower stalks are developing.

The tufted sods vary from 1 to 12 cm. in width, 4 by 5 cm. being an approximate average size. While the smaller clumps have only a few leaves and a single flower stalk, larger ones have an abundant foliage and 20 to 30 stems. In the best stands in the prairie, 15–50 tufts may occur per sq. m., varying in size from single plants to bunches with 10 to 30 stalks. In disturbed areas as many as 80 fruiting heads have been counted in a single clump. In such places, usually as a result of repeated burning, June grass may appear like a thin stand of timothy, but the actual ground cover where it is thickest rarely exceeds 16 per cent. Since this species grows rather erect, the spread of tops is only 1.5 to twice that of the base.

The soft, pliable leaves of this grass are mainly basal and usually numerous. They vary in length from 1 to 4 inches. The cauline leaves are also short, and only three or four in number. None of the leaves usually exceeds 4–5 mm. in width. They roll tightly during drought. An osmotic pressure of 12.5–17.9 A. has been determined for their cell sap, and in drier grassland types, 24.2 A.

The foliage has a general level of only about two-thirds that of the flower stalks which are 20–30 inches tall. Two types of plants occur: the usual type is green and scarcely pubescent, but in the other one the leaf sheaths are very downy pubescent and leaden in color. Like *Stipa*, the flower stalks of this grass stand conspicuously above most of the surrounding vegetation so that its abundance is likely to be overrated.

The densely flowered, contracted, spikelike panicles are 2–5 inches long. Blossoming begins late in May, and the height of anthesis

is reached by the middle of June. By late June or the middle of July, depending upon the season, seeds ripen and the flower stalks and cauline leaves are dry. But even in early autumn the dry tufts of dead stems are conspicuous against the background of browns and

FIG. 21.—Fine clump of *Sporobolus heterolepis* in full bloom; flower stalks about 3 feet high.

greens of the autumnal landscape, although about one-third of the basal leaves are still green.

Koeleria is an excellent forage grass and is relished by all kinds of stock.

SPOROBOLUS HETEROLEPIS

Sporobolus heterolepis, prairie dropseed, is distinctly a bunch-forming grass (fig. 21). It was not found in many areas of the prairie,

notwithstanding its wide distribution. It is always most abundant on the driest uplands, where it may dominate local areas, forming 80 or more per cent of the vegetational cover. More usually it occurs as scattered bunches, intermingling with *Stipa spartea* and *Andropogon scoparius*, where it may constitute from 1 to 20 per cent of the cover. From the hilltops and dry upper slopes it sometimes migrates downward, and large, isolated clumps with unusually developed foliage may occur in areas dominated by *Andropogon furcatus*.

The bunches are usually 4–7 inches in diameter but larger ones up to 18 inches occur. They deteriorate as a result of the death of the central part and often break up into numerous tufts which give the appearance of a loose, open, discontinuous sod. In vigorous bunches, under the higher rainfall of the region, the stems are densely aggregated, as many as 100–200 occurring in a single sq. dm. But under less favorable water content of soil the bunches are only 50–75 per cent filled and the number of stems proportionately reduced. Even then the grass is so dense that other species cannot invade.

An examination of the underground parts indicates that the whole bunch may arise from a single plant. It has many short, woody rhizomes 2–3 mm. thick which occur just beneath the soil surface and give rise to dense clusters of roots. The latter are 1–2 mm. in diameter, very abundant, and somewhat intermediate between those of *Stipa spartea* and *Andropogon scoparius*. As the old roots deteriorate, new ones are produced annually, even in the center of the clump. Branches are very abundant, the whole forming a dense network in the soil. The great clusters of stems with swollen bases, the abundant scales and leaf sheaths, and the inch or more of débris collected in the bases of the bunches are all characteristic.

This species renews growth early and develops rapidly. The foliage reaches a height of 8–15 inches by the first of June. In late summer it varies from 8 to 12 inches in height in very thin soil to 15–18 inches under a better upland water supply. In the lowland the foliage is frequently 2 feet tall or more. The stems are characterized by a distinctly enlarged base. These are tough and hard to cut, hence locally this species is known as "wire grass." By midsummer

each stem has about four green leaves, the basal ones having died. The leaves are 18–42 inches long, attenuated and dry near their tips. They have a breadth of only 2–3 mm. and fold tightly during drought. An osmotic pressure of 9.9 A. was determined in June, but this increased to 28.1 A. during the drought in August. The leaves do not stand erect but curve over gracefully, so that the top of the bunch greatly exceeds the basal area, usually measuring about three times as much. Thus the spreading leaves obscure the bare places between the bunches and the sodlike smaller tufts. Hence in areas of nearly pure *Sporobolus*, where the apparent cover is 80–90 per cent, quadrating shows that the basal area is actually about 10 per cent.

Flower stalks begin to appear about July 1, but anthesis usually reaches its height in late August or September. During years of extreme drought few flower stalks are produced, except about the mounds of gophers or other bare areas where the water content is somewhat increased. Under close competition they may scarcely exceed the leaves in height, but usually they stand well above them. Sometimes the broadly spreading panicles reach a height of 3 feet. They are open and loose and 3–10 inches long. The rather large seeds ripen in September and soon fall to the ground. The shining, light green color and the attenuated leaves with dead tips enable one easily to distinguish the species from *Andropogon scoparius*, which perhaps it most nearly resembles.

This dropseed is palatable to all kinds of stock and furnishes considerable forage when it is not allowed to mature.

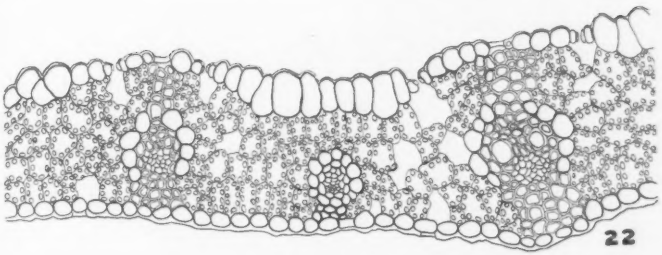
Comparison of leaf structure

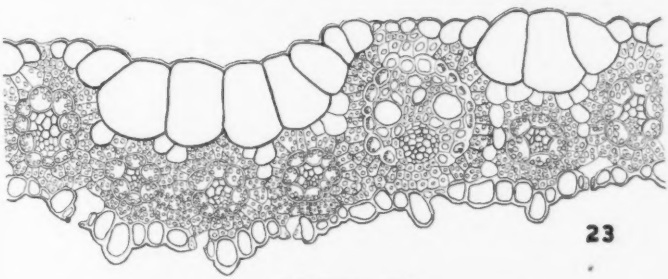
It has already been stated that the length and width of the leaves of the grasses vary greatly. Those of the coarse, lowland species such as *Andropogon furcatus*, *Sorghastrum nutans*, and *Panicum virgatum* are often 2 feet in length and 8–18 mm. wide; consequently the leaf expanse is very large. Upland species have much narrower leaves (usually only 2–5 mm. wide); and as in the case of *Andropogon scoparius*, *Koeleria cristata*, etc., they are relatively short. In some species, however, they are of considerable length (sometimes exceeding 3 feet in *Stipa* and *Sporobolus*), but then they are usually much

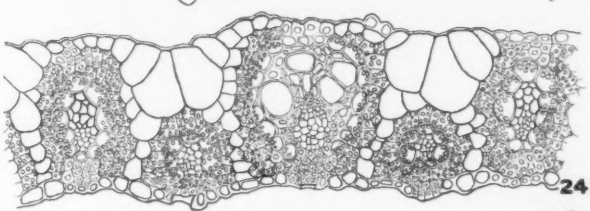
attenuated and often dried at the distal end, so that the area of the individual leaf is comparatively small. It is now our purpose to describe the appearance of the leaves in cross-section, not at length nor in great anatomical detail, but merely to point out several leaf types or patterns and some of the outstanding features of each.

A grass leaf (figs. 22–30) consists essentially of a series of parallel bundles, varying chiefly in size and amount of mechanical and conducting tissue, between which chlorenchyma is supported. Immediately surrounding the bundle is a sheath of cells, often with much thickened, lignified walls. An abundance of mechanical tissue surrounding the vascular bundles protects the water-conducting system from deformation during high winds. Commonly there occurs a second layer of thin-walled parenchyma cells either with or without chlorophyll. Strands of sclerenchymatous tissue ordinarily accompany the bundles and frequently form with the larger ones **I** or **T** beams of mechanical tissue extending across the leaf. The epidermis, especially the lower or dorsal one, is highly cutinized. Over the vascular bundles the epidermal cells are often smaller and thick-walled; while bulliform or motor cells, usually greatly enlarged, occur between the veins. Frequently they lie at the bottom of well defined grooves or occupy the entire thickness of the leaf. They are thin-walled; and when they lose their turgidity through desiccation, the leaf rolls or folds upward or inward. Thus the stomata, which usually occur in rows and ordinarily most abundantly if not entirely in the depressions of the ventral surface, are well protected from water loss. Mechanical tissue is very effective in preventing collapse of the leaf even during wilting and in permitting it to roll. Together with the thick cuticle, it resists excessive bending and twisting before the wind which would result in expulsion of the moist air from the intercellular spaces. The remainder of the leaf is given over to chlorenchyma, except in cases where water-storage tissue occurs.

A comparison of figures 22–30 shows that there are among these dominant grasses three general leaf patterns or types. The first (figs. 22–25) is the *Andropogon* or bluestem type. In this type, *Elymus canadensis* shows the smallest amount of mechanical tissue and the least compactness of the chlorenchyma, as well as the smallest bulliform cells. *Andropogon furcatus* has much larger bulliform







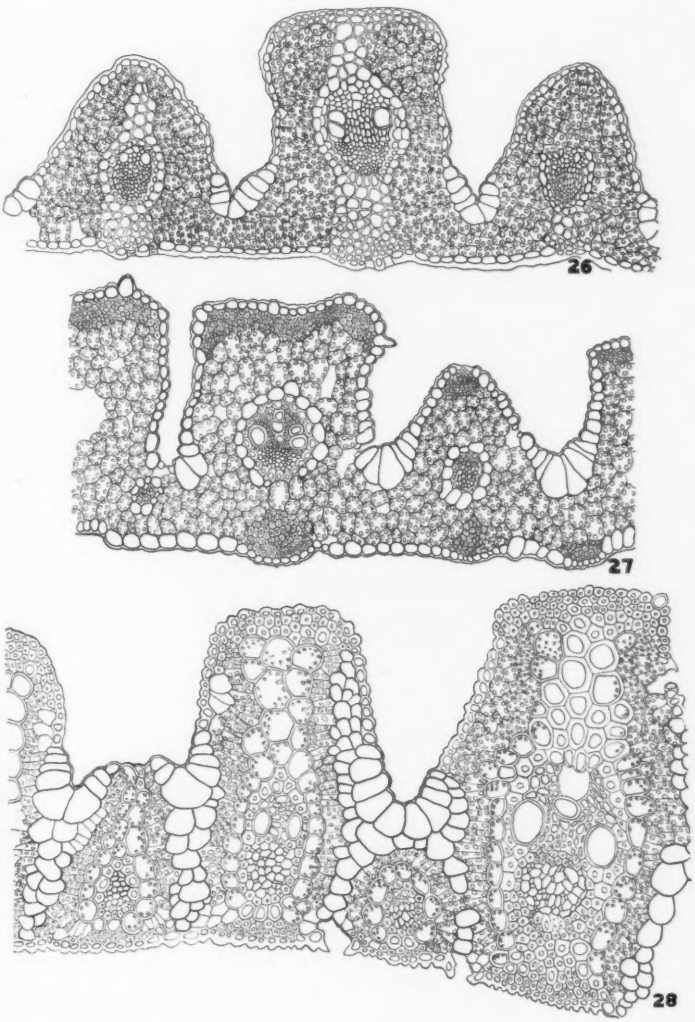
FIGS. 22–25.—Fig. 22, cross-section of leaf of *Elymus canadensis;* fig. 23, cross-section of leaf of *Andropogon furcatus;* fig. 24, cross-section of leaf of *Sorghastrum nutans;* fig. 25, cross-section of leaf of *A. scoparius;* ×150.

cells and more bundles per unit area with a corresponding increase in sclerenchyma. *Sorghastrum nutans* is very similar to *A. furcatus* except that the rows of bulliform cells (as seen in cross-section) are shorter. The leaf of *A. scoparius* is of the same general pattern as the preceding. This narrow leaf folds tightly while the others roll during drought.

Stipa spartea, *Koeleria cristata*, and *Spartina michauxiana* are of the familiar wheat-grass type (figs. 26–28). The leaf is divided into parallel compartments connected by only a few cells of green tissue, with the rolling device prominent in the valleys and the I and T beams well developed. All have a well developed cuticle. In *Koeleria* and *Spartina* especially, water loss is further retarded by layers of hypodermal cells. The depressions in *Koeleria* are often narrower than in the other species, but the supporting tissue in the beams is not continuous. Xeric characters of *Spartina* are even more marked than those of the other two grasses. The epidermis is extremely heavy; the bundle sheaths and accompanying sclerenchyma are more extensive in this thicker leaf; there is more tissue for water storage; and the compartments of chlorenchyma are almost or entirely separated. Indeed the leaf structure is puzzling, considering the usual habitat, until it is recalled that these very long, broad leaves need much mechanical support, and that during dry weather in summer or autumn this rank grass is sometimes subjected to conditions of rather severe drought. Its ability to exist for years as a relict in rather dry soil is due in part to its xeric leaf structure.

The transition from the wheat-grass type to the beaded or grama-grass type occurs in *Distichlis spicata*. This is similar to *Spartina* except that the smaller leaf compartments below the bulliform cells and between the larger leaf divisions are not present, the whole space being occupied by water-storage cells. These effectually segregate the several distinct chlorophyll-bearing compartments of the leaf (figs. 29, 30). The continuity of the water storage sheath about the largest bundles is interrupted by the presence of an abundance of mechanical tissue. The leaf pattern of *Sporobolus heterolepis* is also of the grama-grass type.

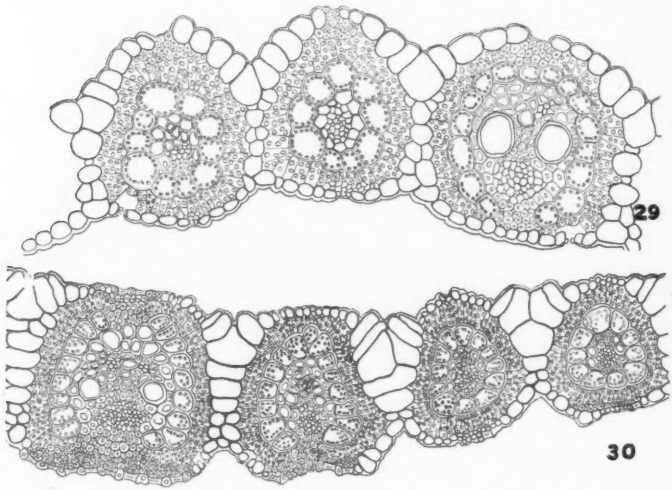
A comparison of figs. 22–30 shows that there is a progressive decrease in the proportion of the leaf used for photosynthesis from the bluestem to the grama-grass type. In *Elymus*, for example, the



FIGS. 26–28.—Fig. 26, cross-section of leaf of *Stipa spartea;* fig. 27, cross-section of leaf of *Koeleria cristata;* fig. 28, cross-section of leaf of *Spartina michauxiana;* ×150.

chlorophyll-bearing tissue is approximately 55 per cent of the cross-sectional area; in *Stipa* it is 51 per cent; but in *Bouteloua racemosa* it falls to only 44 per cent.

All of the leaves exhibit morphological structures characteristic of grasses of arid climates although in some these are less marked than in others. The leaves of even the least xeric, as regards water



FIGS. 29, 30.—Fig. 29, cross-section of leaf of *Panicum virgatum;* fig. 30, cross-section of leaf of *Bouteloua racemosa;* ×150.

content of soil, are regularly subjected to dry, hot winds during certain periods. The leaves of *Andropogon scoparius* and *Sporobolus* fold tightly during drought; all of the other leaves roll.

Summary

1. A study of the tall-grass prairie from southern South Dakota to northern Kansas and eastward into Iowa reveals several patterns or types of vegetation. The big bluestem type is the most extensive and the most important of those found on the lowlands. It is characterized by the single species, *Andropogon furcatus,* which alone often constitutes 80 or more per cent of the vegetation. *Sorghastrum nutans* is a close ecological equivalent which associates with it, but it is in general much less important.

2. *Spartina michauxiana* covers extensive areas of wet, poorly aerated soil with tall, dense, and often nearly pure stands. *Panicum virgatum* and *Elymus canadensis* form an intermediate lowland type of much less extent than either of the preceding.

3. *Andropogon scoparius* constitutes the most extensive upland type and easily exceeds in importance all other upland species combined. *Stipa spartea* is the dominant of another upland type found on steep slopes and ridges in the central and especially the northern part of the area. *Sporobolus heterolepis* exhibits a minor, dry upland pattern. *Bouteloua racemosa* is a minor constituent of all the grassland types, except *Spartina*, occurring less abundantly in the most xeric ones. *Koeleria cristata* is intermixed with *A. scoparius*, *S. spartea*, and *S. heterolepis*, thus showing a preference for dry uplands.

4. The lowland species, except *Elymus* and *Bouteloua*, are sod formers; those of the upland are bunch formers, although *Andropogon scoparius* regularly forms sod-mats under favorable conditions. *Elymus* and *Bouteloua* form either bunches or a poorly developed sod.

5. The chief "weapons" of competition of the tall, lowland dominants are their ability to endure shade and the rapid development of rhizomes resulting in the formation of a dense sod. Upland species rely upon successful competition for water and ability to withstand drought.

6. The seedlings of all species develop rapidly, tiller freely, and under favorable conditions without competition may produce seed the first summer, although under natural conditions two and often three years are required.

7. Root depths of 1.5–3 feet are attained the first season by various lowland species and 1–1.5 feet by those characteristic of upland. Mature root systems of lowland species are likewise in general deeper (4–10 feet) than those of the drier upland soil (1.5–5.5 feet). Those of lowland are much coarser and usually penetrate more vertically downward, however, while those of upland are fine, profusely branched, and widely spread.

8. *Stipa* and *Koeleria* begin growth in March, blossom in late May or June, and make a renewed growth in autumn. *Elymus* likewise starts growth in March; the other species about the middle of April.

Anthesis begins in late July and reaches its height in August or early September.

9. Three general types of leaf structure are evident: the bluestem type, including *Elymus;* the wheat-grass type exhibited by *Stipa*, *Koeleria*, and *Spartina;* and the grama-grass type as shown by *Bouteloua*, *Panicum*, and *Sporobolus*. All show pronounced xeric structures.

10. Osmotic pressures in the various grasses varied from 7.5 to 14 A. during the spring and early summer when the water supply was abundant and growth vigorous. No consistent differences between upland and lowland species were found, but during a severe summer drought the more xeric species showed about twice the osmotic pressure of those of lowlands. These ranged from 22.4 A. for *Stipa*, 24.2 A. for *Koeleria*, and 28.1 A. for *Sporobolus* to 30.4 A. for *Andropogon scoparius*. *Panicum* gave a pressure of 13.7 A. and *Andropogon furcatus* of only 14.5 A. Other lowland species gave somewhat similar results, relict *Spartina* reaching a maximum of 16.4 A. Thus there seems to be a clear relationship between water content of soil and osmotic pressure of the cell sap, species of the drier soils developing the higher osmotic pressures.

11. All of the dominant grasses have excellent forage value, especially if they are grazed or cut for hay before the coarse flower stalks of the late-blooming species become hard and fibrous.

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[*Accepted for publication October 2, 1931*]

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STRUCTURE OF SEEDLIKE FRUCTIFICATIONS FOUND IN COAL BALLS FROM HARRISBURG, ILLINOIS

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 431

HARRIETTE VALLETTA KRICK

(WITH TWENTY-ONE FIGURES)

Introduction

The attention of English and French paleobotanists was early directed to the study of certain seedlike fossils, occurring in the form of impressions and casts in the shales above the coal seams, and as petrifactions (coal balls) in the coal seams themselves. LINDLEY and HUTTON (**20**) ascribed the 3-angled *Trigonocarpon* to palmlike plants similar to the Chilian *Micrococos*. BRONGNIART (**12, 13**) and WILLIAMSON (**42**), studying the cellular anatomy, found a similarity between the structure of the Paleozoic seeds and the seeds of cycads and *Ginkgo* of the present day flora. On the basis of anatomical investigation not concerned with the organs of reproduction, POTONIÉ (**30**) applied the name Cycadofilices to the group of fossil plants showing characteristics common to pteridophytes and gymnosperms.

In 1903, when OLIVER and SCOTT (**29**) announced that a certain characteristic seed, *Lagenostoma*, belonged to the fernlike fronds of *Lyginodendron oldhamium*, the name Pteridosperms was proposed for that group of Cycadofilices which bore seeds. Further research proved the two terms to be almost coextensive, so that by many they have come to be used as synonyms (**36**). Many of the flattened seeds were established, through the researches of GRAND 'EURY (**14, 15**), RENAULT (**32**), BERTRAND (**11**), and ARBER (**1**), as the fructifications of Cordaitales. From a similar study (**34, 35**), *Lepidocarpon* was recognized as a seedlike reproductive organ of *Lepidodendron*, not included in the Pteridosperms of SCOTT. Between the years 1903–1916, additional work by BERTRAND (**4–9**), OLIVER (**26–28**), SCOTT (**37**), and their pupils greatly increased our knowledge of the structure of these seeds, but very few cases have been found of

continuity of reproductive and vegetative structure, so that actual identity could be established beyond all doubt.

SEWARD (**38**) classifies the 29 genera so far discovered into three main groups upon the basis of structure: (1) Lagenostomales, radially symmetrical, with integument and nucellus undiverged as in modern cycads; (2) Trigonocarpales, radially symmetrical, with integument and nucellus completely diverged except at the chalazal disk; and (3) Cardiocarpales, with the seeds more or less flattened in cross-section. A broader terminology (**24**) designates the first two as Radiospermeae, the latter as Platyspermeae. During this time little work was done in America on the structure of such fructifications, and nothing was done in the study of the petrifactions.

At about the time that BRONGNIART and WILLIAMSON were working, NEWBERRY (**22**) published a description of seeds found in coal beds of Ohio. In his discussion of the subject, based upon observation of casts and impressions, he states that *Trigonocarpon* is a nut of a drupaceous fruit, probably belonging to *Sigillaria*. Clearly he thought of these as fruits rather than seeds. He records "detached portions of the external skin or coating bearing the impression of the stem at the base, of the flower above. The latter is sometimes a six-rayed star, such as we might suppose would be left by the fall of a six-parted flower."

LESQUEREUX (**19**) catalogued species of *Trigonocarpus*, *Cardiocarpus*, and *Rhabdocarpus* from the coal fields of Pennsylvania, Ohio, Illinois, and various other localities in the United States. He admits that the impressions are poor bases for determining the true character of the seed. His terminology is disconcerting: he speaks of the outside layers of the seed as being "composed of various superposed layers, sarcotesta, pericarp, and endocarp." He indiscriminately designates the fossils as nuts, fruits, and seeds. WHITE (**39, 40**) reported large seeds from Missouri and later made an extensive report on seeds found upon the fronds of *Aneimites* (*Adiantites*) from West Virginia. NOÉ (**23**) found several genera in northern Illinois.

With the finding of similar vegetative structures in the Coal Measures of America and Europe (**17, 31**), it seemed worth while to investigate the petrified material for an anatomical study of seed-like structures in the coal balls of America. With this idea in mind, the writer undertook the minute observation of the coal balls which

were brought into this laboratory by Dr. Noé. The findings resolved themselves into three points of major interest: (1) a study of serial sections for the identification of the seedlike fructifications from Harrisburg; (2) a morphological interpretation of the material identified; and (3) an environmental theory for a closer correlation between casts, impressions, and petrified material.

Methods and material

The materials used as a basis for this study were from coal balls gathered from coal no. 5 of the O'Gara Mine at Harrisburg, Illinois. Systematic cutting of the coal balls resulted in serial sections 15×10 cm., varying from 2 to 5 mm. in thickness. From these sections thin slides suitable for use in microscopic study were prepared, following two general methods.

I. The older method consisted in grinding the thick sections with carborundum powder on a rotating metal disk or on a glass plate. This took many hours of labor and some skill to obtain the proper uniform thinness. It is obvious that in this process entire seeds of small diameter could be entirely overlooked unless careful watch was constantly maintained. The loss which was incurred through the cut of the saw and the subsequent grinding often left little clue for identification. Of the seeds dealt with in this paper, the larger longitudinal sections of *Trigonocarpon parkinsoni* were prepared successfully in this way, as were also several sections of *T. pusillus* and *Lepidocarpon lomaxi*, which were imbedded in a softer matrix which cracked readily. From these, celloidin films could not be taken because the solvent used dissolved the mounting medium.

II. The celloidin film method was devised by Koopmans in collaboration with Walton (**18**) in 1928, and is now being used by Leclerq, Gordon, Hemmingway, and others with satisfactory results. In its simplest terms it involves the following steps:

1. Smooth the surface with carborundum powder of medium grain.

2. Wash thoroughly in running water to remove all particles of carborundum.

3. Etch with acid (hydrochloric acid for calcareous material; hydrofluoric acid for siliceous material). Varying strengths of acid were found to be necessary, according to the composition and con-

sistency of the coal ball. GORDON and HEMMINGWAY recommend a very dilute acid for only a very few seconds. In this laboratory it was found that when considerable pyrite was present, a 10 per cent solution acting for 1–2 minutes was not any too strong to give a desirable etching depth, while in other instances a 5 per cent solution acting for just a few seconds was sufficient. When several cuts from the same coal ball were to be etched, time and material were saved by pouring the acid over the specimens in a shallow tray, as for developing plates, and gently rocking the tray until the desired degree of etching had been obtained. A similar tray was also used for the next step.

4. Wash in gently flowing water to remove all acid, taking care to preserve the organic particles intact.

5. Dry in an oven or open place undisturbed by dust particles. This leaves the bits of carbonaceous material free to be imbedded by the celloidin film.

6. Pour on the solvent to dehydrate and remove all air bubbles.

7. At once pour on the cellulose solution. The European workers use for this a solution of cellulose in amyl acetate or acetone, but here celloidin in ether-alcohol, as suggested by PETRY, was found to be much more effective. Solutions of 4–6 per cent were used.

8. When dry, and before the film begins to wrinkle away from the surface, it can be peeled off and placed between two glass plates in order to maintain a smooth surface. It may be mounted immediately in balsam or it may be used as it is.

The advantages of this later method are obvious, in taking much less time, in obtaining many more sections, and in reducing the waste and uncertainty which is encountered in the making of serial sections by the old method.

To complete the study, reconstructions were made following the method outlined by SALISBURY (**33**).

Harrisburg seeds[1]

A survey of the genera found in the Harrisburg coal balls thus far does not present a great variety when compared with the number

[1] Use of the term seed usually implies not only the permanent retention of the megaspore within the megasporangium, but, that which is more essential, the presence

given by SEWARD (38). From the coal balls of Harrisburg so far cut, four genera, represented by five species, have been identified. Of these, one, *Lepidocarpon*, belongs to a plant whose sole survivors today are classed among the spore-producing pteridophytes. The remainder are truly gymnospermous in character. It is well to keep in mind, however, that this collection deals with coal balls from a single locality, whereas the one mentioned by SEWARD consists of a composite report from many localities.

Lepidocarpon lomaxi Scott.—Of all the seedlike fructifications found in the Pennsylvanian, *Lepidocarpon* represents the most unique. It is one of the most easily recognized seeds in our coal balls, as well as the most abundant.[2] Essentially it consists of an elongated sporangium borne on the adaxial surface of the pedicel of a lycopodaceous sporophyll. These sporophylls are borne in cones much like *Lepidostrobus*, but all of the specimens so far found are not attached to the original axis.

The sporangia are usually more massive than in the male cones of a similar nature, although the structure of the sporophyll is essentially the same in the very young condition. Later, however, the free edges of the pedicel appear to grow upward as a delayed lamina, leaflike in character, which completely surrounds the sporangium except for a longitudinal slit along the upper face. In tangential section, as shown in fig. 1, such a structure bears close resemblance to a gymnosperm seed, with a massive nucellus, the leafy lateral emergences of the pedicel appearing as an integument, the slit along the upper side as a micropyle. It was such a section that WILLIAMSON (42) describes as *Cardiocarpon anomalum*.

Parallel to the sporophyll pedicel, as seen in fig. 2, the sporangium is 8–10 mm. in length. At the proximal end of the pedicel the sporangium is less than 2 mm. in cross-section, reaching 5 mm. at the distal

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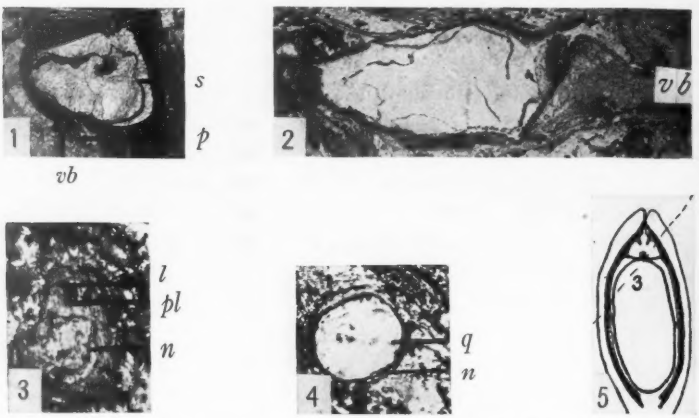
of an embryo with its stored food. In the absence of embryos in the Paleozoic, structures with a thinner megaspore membrane, inclosed by a massive nucellus and surrounded by an integument, have been called seeds. To conform with the English and French descriptions, such use of this term has been retained in this paper.

[2] Besides the material mentioned in this paper, Dr. FREDDA D. REED has found specimens of *Lepidocarpon* in coal balls from Harrisburg and Indiana. Miss INEZ CLARK also reports it from Harrisburg coal balls with which she was working. I have found it in material from Danville, Illinois.

end. In height it varies from 5 to 8 mm. above the surface of the sporophyll. These measurements approximate the range of size given by SCOTT (**35**) for *Lepidocarpon lomaxi*.

Closely pressing against the inner face of the sporangium is found the thin megaspore membrane, within which the prothallus has been found in some of the English specimens. The sporangium has never



FIGS. 1–5.—Fig. 1, *Lepidocarpon lomaxi:* tangential view showing similarity in structure to ovule with integument; *s*, sporangium wall with megaspore membrane on inner surface; *p*, pedicel of sporophyll with lateral laminal emergence forming covering of sporangium except for slit at top; *vb*, position of vascular bundle. H 210; ×5. Fig. 2, *L. lomaxi:* section taken obliquely parallel to sporophyll pedicel; upturned lamina of sporophyll seen at larger distal end. H 213; ×5. Fig. 3, *Conostoma oblongum:* oblique longitudinal section from micropylar end; *l*, remains of lagenostome; *pl*, plinth cavity; *n*, nucellus. H 213; ×10. Fig. 4, *C. oblongum:* cross-section through basal portion showing remains of gametophyte tissue within undiverged nucellus and integument (*g*). H 213; ×10. Fig. 5, reconstruction of median longitudinal section of *Conostoma oblongum* from Harrisburg material; ×7.

been found with any indication of a dehiscence slit, and from the nature of the megaspore membrane it is supposed that the single functional megaspore with its prothallus was permanently retained within the megasporangium during development of the young embryo. In such a sense, this has been called a seed by SCOTT (**35**) and others, although its early development could hardly be recognized as an ovule. Since none of the lycopods of the present day show this

near approach to the seed habit, *Lepidocarpon* is of interest as demonstrating one way in which the seed habit may have originated; although it is not necessarily in the direct evolutionary line of the higher seed plants.

Conostoma oblongum Williamson.—This is a slightly 6-angled seed having an average length of 5 mm. and width of about 2 mm. Its extremely small size limits any extensive study of its structure, both by reason of the small number of sections which may be obtained and the large proportion of body length which is lost in the cut of the saw. Of seven sections obtained from the Harrisburg material, only a single instance was found of a cut made so as to show any of the characteristic micropylar structure, and this, because of the obliquity of the cut, does not show the lagenostome (fig. 3).

As is characteristic of the Lagenostomales, the integument and nucellus are undiverged except for a short distance at the micropylar end. The upper portion of the nucellus, which in the other seeds studied makes up a thickened cellular, more or less elongated nucellar beak, is here a lens-shaped cavity with epidermal layer intact. The term "plinth" has been applied to this peculiar structure by English investigators (**28**). A remnant of the cellular tissue, which at one time may have completely filled the cavity, is present in only a single cushion-shaped mass near the center of the septum which separates the plinth cavity from the larger megaspore cavity below (fig. 5).

In oblique transverse sections taken near the base, such as the one shown in fig. 4, the integument is composed of two kinds of tissue. The outer is a single layer of palisade cells, with cell contents densely carbonized; the inner is a wider layer of cells more or less sclerotic in nature, elongated in a longitudinal direction. In the preservation the nucellar cells, large and conspicuous, are occasionally still in the original state of lack of divergence from the integument.

Trigonocarpon pusillus Brongniart.—This is a slightly 3-angled, unribbed seed, 12 mm. long and 6 mm. wide, apparently with three distinct layers to the integument. The outer parenchymatous layer is but six or seven cells wide, 0.3–0.6 mm. thick, bounded externally by a thick-celled epidermal layer. Mucilage or resin canals, schizogenous in nature, are numerous in this outer layer (figs. 6, 7). Be-

tween any two adjacent angles, a single vascular bundle is found. Immediately inside of this is a broad band of parenchyma cells 0.3 mm. thick, essentially like the first except that the cell cavity contains a dense mucilaginous or resinous substance which makes it appear in the petrifaction as a coaly layer. Within this is the third layer, 0.2 mm. thick, of cells thickened as typical stone cells. In mass these latter two layers appear as a single one, although in places they are often separated through pressure (fig. 7).

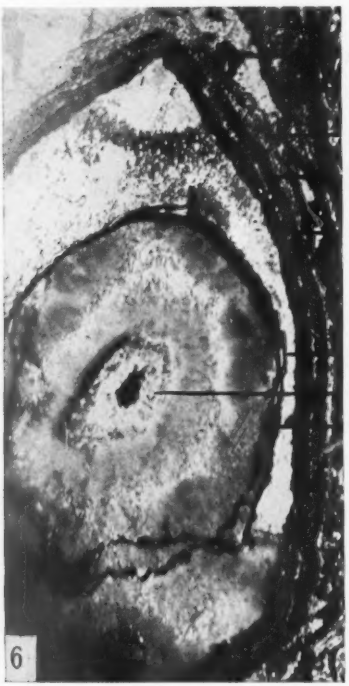


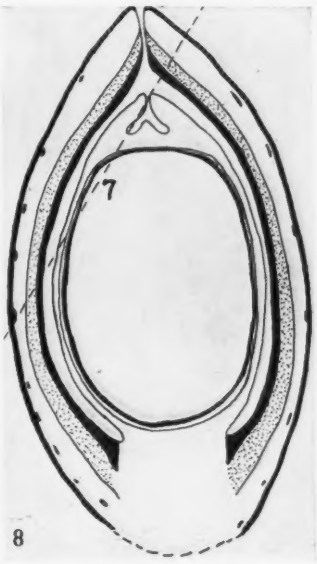
FIG. 6.—*Trigonocarpon pusillus:* longitudinal oblique section showing three layers of integument; *sa*, sarcotesta with epidermis (*ep*); *m*, mucilage canal; *pa*, parenchyma with dense cell contents, coaly layer; *sc*, sclerotesta; *n*, wrinkled nucellus; *mg*, megaspore membrane; *g*, gametophyte remains. H 214; ×10.

The nucellus, greatly wrinkled in the basal portion, consists of a definite epidermal layer of cells elongated in a longitudinal direction, with less distinct cellular tissue within. Its only connection with the integument lies in the chalazal disk at the base. In sections nearly longitudinal (fig. 6) the megaspore membrane shows up in striking contrast to the nucellus, the former being a dense, opaque orange when etched with hydrochloric acid; the latter a clear amber. At the micropylar end the nucellus shows a centrally placed pollen chamber (fig. 7).

The matrix in which this seedlike structure was imbedded was so heterogeneous that it is a little hazardous to connect it with any given plant. Cordaitean leaves were present as well as good speci-

mens of Medullosean petioles, *Sphenophyllum*, and stigmarian roots.

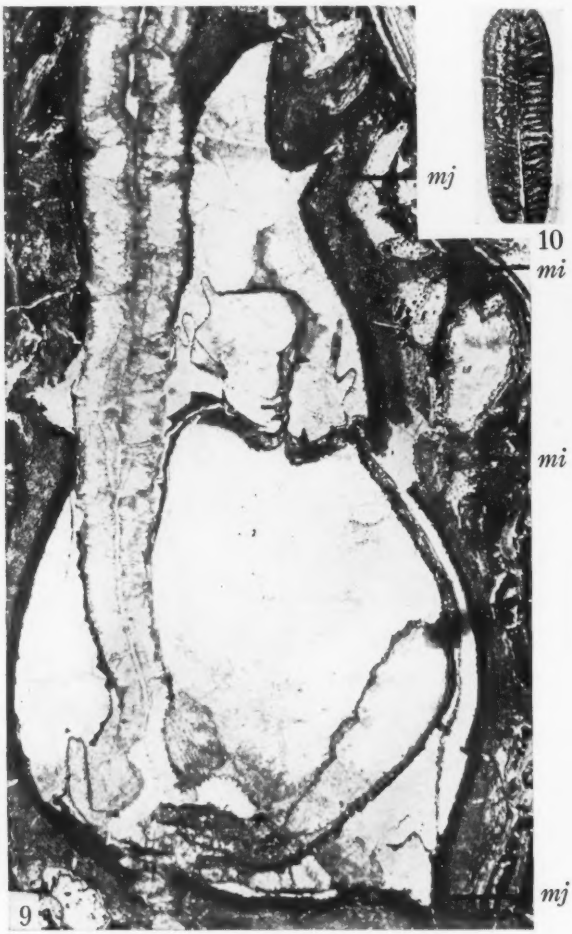
Trigonocarpon parkinsoni Brongniart.—This seed, the largest found in the Harrisburg material, is an elongated ovoid body 3–4 cm. in length and 2–2.5 cm. in width. In cross-section in the early stages it is roughly circular in outline, while later the twelve longitudinal ribs of the middle integument layer give it a sharply ridged contour. Of these ribs, the three more prominent are the major and the nine less prominent are the minor ribs. They are arranged in a definite sequence, with three minor ribs lying between any two adjacent major ribs (fig. 9).



FIGS. 7, 8.—*T. pusillus:* section near micropyle showing pollen chamber of nucellus in addition to these features. H 214; ×10. Fig. 8, reconstruction of median longitudinal section of *T. pusillus* from Harrisburg material; ×7.

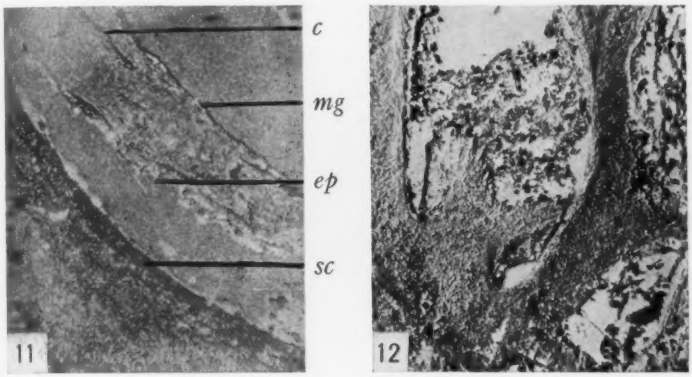
Two specimens formed the basis of study, and since they showed somewhat different stages of development, they give a clue to the progressive changes taking place in the maturation of the seed coat and the breakdown of the nucellus. At first glance the shape of the seed is suggestive of the Platyspermeae, but closer observation shows

this to be the result of lateral compression during fossilization. This process has not interfered with the excellent preservation of the cellular structure. The integument shows early differentiation into



FIGS. 9, 10.—Fig. 9, *Trigonocarpon parkinsoni:* cross-section from older seed showing *mj*, major ribs with minor ribs (*mi*) between. H 213; ×5. Fig. 10, leaf of *Medullosa* (*Alethopteris*) taken parallel to surface, showing venation. H 213; ×10.

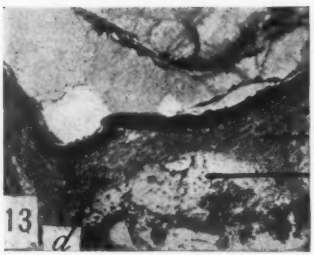
three layers of tissue: the outer, sarcotesta; the middle, lacunar sclerotesta; and the inner, compact sclerotesta. The parenchymatous sarcotesta, less than 1 mm. in thickness, is bounded externally by the small epidermal cells and several rows of thickened hypoderm. In this region lie the six vascular bundles which supply the integument. The inner margin of the sarcotesta merges gradually into a wider layer of lacunar tissue, sclerotesta, which makes up the

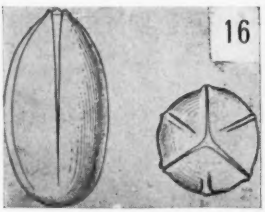


FIGS. 11, 12.—Details of nucellus and integument of *T. parkinsoni:* fig. 11, from younger seed showing undifferentiated outer layer of integument; *sc*, sclerotesta already differentiated; nucellus shown with epidermis (*ep*); *c*, conductive tissue of nucellus; *mg*, megaspore membrane. H 213; ×15. Fig. 12, same, taken through chalaza. H 213; ×10.

framework of the ribs. In median cross-section this layer is 2 mm. in thickness, extending out for 4 mm. in the region of the major ribs. In the later stage it is composed of cells, sinuous and irregular in shape, although in the earlier stage, as shown in fig. 11, the cells are isodiametric. The major ribs in the upper third of their length show a marked development of enlarged, thickened, intracostal cells (fig. 13) which mark the line of dehiscence of the seed in germination. An interesting correlation exists in the development of the integument layers and the structure of the nucellus. In the seed in which the integument appears to be in a younger condition, judging from the size and maturity of the cells, the nucellus is massive with a distinct epidermis, and has 8–12 conductive strands which

extend from the basal disk of sclerotic tissue up to the floor of the pollen chamber. The megaspore membrane is evident, tightly adhering to the inner wall of the nucellus. In the older, judging from





FIGS. 13–16.—Fig. 13, cross-section of major rib of older seed showing three layers of integument; *sa*, sarcotesta; *la*, lacunar sclerotesta; *sc*, sclerotesta; *d*, enlarged thickened intracostal cells marking line of dehiscence of seed during germination; *n*, nucellar remains. H 213; ×10. Fig. 14, reconstruction of *T. parkinsoni* from Harrisburg material (median longitudinal section). ×2. Fig. 15, cast of *Trigonocarpon* after NOÉ; about natural size. Fig. 16, cast of *Trigonocarpon* after ZEILLER, showing infiltration through dehiscence slit; about natural size.

its more mature middle integument layer and dehiscence slits, the nucellus is more wrinkled and thinner, in some places only the epi-

dermis being left. The megaspore membrane was not to be found. In comparison with the present day seeds, this has striking resemblance to one from which the embryo has germinated, leaving only the remains of the nucellus within the seed coat.

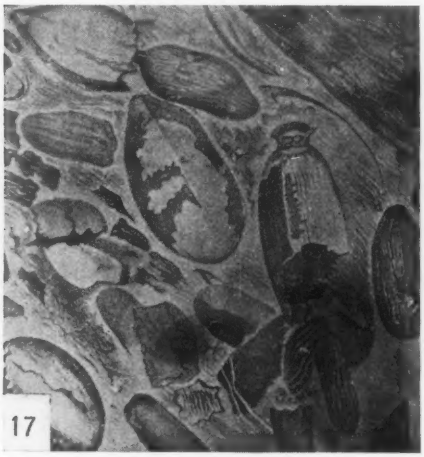
These seeds, both in size and structure, agree well with the *Trigonocarpon olivaeforme* described by WILLIAMSON (**42**), and later by WILD (**41**), who found them to have a longer micropyle than had been ascribed to them formerly. Later the same material, reinvestigated by SCOTT and MASLEN (**37**), was included under the species *T. parkinsoni*. While the present material lacks the elongated micropyle and sarcotestal "wing" reported by SCOTT and MASLEN, such a discrepancy could so easily be attributed to the preservation that I find no grounds for making a new species.

Reproductive organs described from casts by NOÉ (**23**) as *Trigonocarpon rostratum* Brongniart may represent casts of the external surface of such a *Trigonocarpon* with the sarcotesta removed or dried down in the process of fossilization. The nutlike internal casts of this species are among the most numerous fossils found in the Coal Measures.

The petrifactions described here as *Trigonocarpon parkinsoni* were imbedded in a matrix of leaves and petioles of *Medullosa*. One of the leaves is shown in fig. 10. Since they represent the best preserved specimens found in any of the coal balls, it is supposed that they had not been carried far from the parent plant. Although no actual attachment of leaves or petioles to seeds has been found, the homogeneity of the matrix and certain structural likenesses strongly suggest that these reproductive organs belong to *Medullosa*.

Stephanospermum akenoides Brongniart.—The *Stephanospermum* found in the Harrisburg petrifactions is much like that described from the English (**24**) and French (**12, 13**) coal balls. It is an elongated ellipsoid seed about 10 mm. in length and 5 mm. in greatest width. The crown of tissue which surrounds the micropyle rises for over a millimeter above the body of the seed (figs. 18, 19), and surrounds the micropyle, leaving a shallow perimicropylar trough less than 1 mm. in width. The testa consists of a double layer: the inner, 0.1 mm. thick, of longitudinally elongated cells which extend into the micropyle and form the core of the crown; and an outer wider

region 1 mm. thick of palisade-like cells with its long axis at right angles to the surface. Near the micropylar trough the micropyle appears slightly 6-angled, and sections near the base of the seed have somewhat the same appearance, while a median transverse section shows it to be almost circular in outline. The nucellus is poorly preserved (figs. 19, 20). Although much wrinkled and plasmolyzed, longitudinally elongated epidermal cells could be distin-



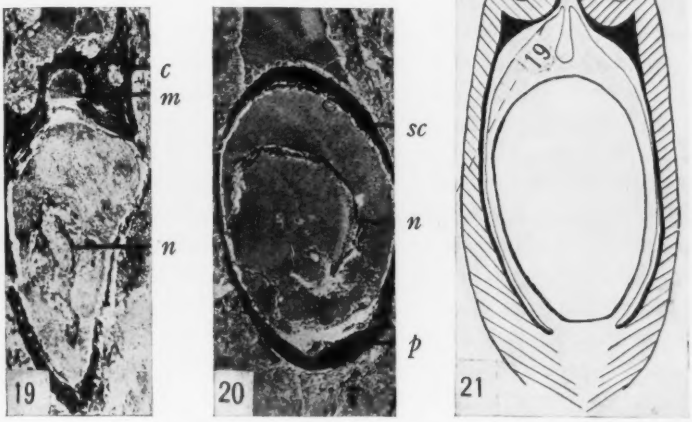
FIGS. 17, 18.—Fig. 17, impressions of sclerotesta and nucellus from seed remains of *Trigonocarpus*, after NEWBERRY. Fig. 18, longitudinal oblique section of *Stephanospermum akenoides* showing *m*, micropyle; *c*, crown of integument surrounding micropyle; *p*, palisade layer of integument; *sc*, sclerotesta; *n*, nucellar remains. H 215; ×10.

guished, within which the megaspore membrane lay. No clue to the identification of the parent plant has as yet been discovered in the petrifactions. Casts may be among those designated as *Rhabdocarpus*.

Morphological interpretation of seeds

Somewhat arbitrarily, perhaps, the term seed has been used in the foregoing descriptions rather than the terms fruit and nut of the earlier writers. According to the present day conception, a fruit is the seed-bearing product of the plant. This may consist of only the ovary or part of the ovary, or it may consist of other accessory parts

such as leaves (sporophylls), bracts, receptacle, etc. A nut is a type of fruit "hard indehiscent, 1-celled and 1-seeded" (**16**). From the descriptions it is evident that, with the possible exception of *Lepidocarpon*, an ovule with its single integument matured into several layers is all that is involved in the final structure. For this reason the term seed has superseded the terms fruit and nut in recent literature. A further question, however, presents itself as to the stage of development of these seeds: Are they true seeds in which



FIGS. 19–21.—Figs. 19, 20, longitudinal oblique sections of *Stephanospermum akenoides* (see legend for fig. 18 for details). ×10. Fig. 21, reconstruction of median longitudinal section through *S. akenoides* from Harrisburg material. ×7.

the embryo has not been preserved, as believed by BRONGNIART and RENAULT, or are they the younger stage known as the ovule?

In ontogeny the development of a seed is a dynamic process, beginning with the early growth of a nucellar mass, and passing into the stage of an integumented nucellus, within which the megaspore mother cell is differentiated. Up to this time the cells are meristematic, and may be said to be in a free, independent state. Beginning with the megaspore, accompanied sooner or later by development of the gametophyte structure, there is found a state of dependence of certain cells or groups of cells upon others. The first instance of this

is in the enlargement of the megaspore, when the tissues of the nucellus adjacent to the megaspore membrane are crushed and their contents assimilated by the developing megagametophyte. Later this is carried still further, in the dependence of the sporophyte upon the food material stored in the megagametophyte. In the early stages up to fertilization, such a structure is known as an ovule, and later as a seed.

When we think of the special care which must be taken in gathering material in the young stages of the present day plants for critical study of the reproductive organs, it is not surprising that embryo material is not found among the meager representatives which have been handed down from the abundant gymnosperm flora of the Paleozoic period. The chances are exceedingly small that such young tissue would break away from the parent plant, and it is only such material as might have undergone normal abscission that is ordinarily preserved. To pass to the other end of the life cycle, which is in the ordinary conception of the seed the most important; the greater part of the life cycle is concerned with the nourishing of the embryonic sporophyte. But in not a single seed found from the Paleozoic has there been any evidence of an embryo. Numbers cannot account for this, for in all the studies that have been made of some hundreds of specimens, none has given the slightest evidence of any stage of an embryo. A certain uniformity of structure prevails throughout. All seem to have been derived from orthotropous ovules. The integument may be diverged early (*Conostoma*) or late (*Trigonocarpon*), but in either case the cells constituting it reach maturity early, as is reported for living gymnosperm seeds. The integument differentiates into two and sometimes three intergrading zones: the outer, sarcotesta, usually rather poorly preserved; the inner, sclerotesta, composed of compact fibrous tissues, usually much thickened as stone cells. In the earlier stages the nucellus is a rather massive structure, with definite epidermis of cells rounded in cross-section, somewhat elongated longitudinally, and with densely colored cell contents. It is always more or less wrinkled into deep folds as in a much plasmolyzed state. In its turgid condition it probably entirely filled the testal cavity, taking its contour from the pressure of the inner margin of the sclerotesta. The upper portion of the

nucellus was differentiated into a beaklike chamber in which pollen is sometimes found (**3, 27**). Within the nucellus the megaspore membrane is usually still present, closely following its inner margin. Gametophyte tissue is not as well preserved in the present material as in some of the English specimens (**21**), but is represented by a brownish mass of crystalline material occupying the center of the megaspore (**10**). The whole suggests a poorly preserved ovule of the cycad type, with a megagametophyte in a starchy gelatinous mass, just after the delicate cell walls have begun to come in.

Where the nucellar pollen chamber shows little breakdown of tissue, this structure should be interpreted as an ovule, perhaps abortive, perhaps only a normal stage in the life cycle which did not develop further because of the unfavorable conditions under which it happened to fall during the infiltration process. Some, with a thinner nucellar membrane, a beaklike projection of the nucellus into the micropyle, and a sclerotesta which shows the longitudinal splitting of the stony layer into valves with little or no sarcotesta left, represent a later stage in the ontogeny of the seed, where the embryo has escaped, leaving only the shell of the integument and nucellus behind. Such remains are found abundantly as casts (fig. 15 *a*, *b*). These, since they are of a much later stage but yet are indicative of their early seedlike nature, might best be designated as seed remains. With the earlier and later stages thus preserved, it is conceivable that we may yet find a seed, in the strictest sense of the term, with an embryo preserved, if a sufficient number of specimens in the form of petrifactions, casts, and impressions are carefully observed.

Environmental theory for correlation of casts and impressions with petrifactions

While it is not always safe to assume that similar appearances constitute a basis for relationship, it has been generally recognized (**2**) that, in the case of *Trigonocarpon* at least, a number of fossils produced by various forms of fossilization have been discovered to be so nearly alike as to be given the same species name. The method of preservation of each of these forms has been explained, but no adequate theory has been proposed to account for their correlation.

From the study of the morphology of such material as was available, a suggested theory, based upon ecological factors, has been formulated and will briefly be outlined.

All the ovules and seed remains show a constant, clearly defined abscission from the parent stalk which bore them. The integumental covering matured early, differentiating while it was still attached to the parent plant, even carrying the beginnings of the dehiscent mechanism. It is assumed that these seed-bearing plants, growing at or near the margin of the swampy arm of the sea, carried a hereditary factor for dropping the ovules early in their life history, at or near the time for pollination. Some of these, pollinated or unpollinated, fell into the deeper, still, brackish water. Further development of the ovule and subsequent germination was thus prevented. The nucellus was badly wrinkled through the plasmolyzing action of the brackish water, although the cells making up the whole were usually well preserved, free from bacterial action. These, imbedded in the organic remains making up the coal seam, are usually found in the coal balls (petrifactions of coal seams). Sometimes such ovules fell on the muddy surface of the soil near the base of the plant, and their impressions were preserved, without the sarcotesta. In other cases pollination had been completed and an embryo formed which had germinated and escaped. Only the seed remains were left, often seen as valves (two in the case of *Cardiocarpon*, three in *Trigonocarpon*). The nucellus may be left as a thin papery layer not greatly wrinkled. It is through the micropylar opening that the sand and clay entered and formed such characteristic casts as those shown in fig. 15. It was the micropylar end of the nucellus, or possibly even a structure corresponding to the coleorhiza of the present-day cycads, that NEWBERRY saw and described as the 6-rayed star, the remains of the floral parts. These remains are now found as casts in the roof nodules of the coal seams or as impressions in the shale deposits formed by the sediments which flooded the gradually subsiding Coal Age swamps.

Summary

1. Certain rounded, flattened, or angular seedlike objects appearing as casts or impressions in the shale above the coal seams of the

Pennsylvanian in America have been designated as fruits, nuts, or seeds, in spite of the absence of structure-showing material. Such fructifications offering structure are now at hand from coal balls from coal no. 5, O'Gara Mine, Harrisburg, Illinois. Using the older method of thin rock sections and the newer one of KOOPMANS-WALTON, serial sections were obtained which formed the basis of a morphological study of the following species:

a. *Lepidocarpon lomaxi* Scott.—An elongated sporangium borne on the adaxial surface of the leaf (sporophyll), the outgrowing edges of which close up around the sporangium to form the integument; length 10 mm.; width of distal end 5 mm., proximal end 2 mm.; height 5–8 mm.; definitely identified as the fruiting structure of a *Lepidodendron*.

b. *Conostoma oblongum* Williamson.—An ellipsoid integumented ovule, 5 mm.×2 mm.; integument of two layers: outer, palisade; inner, longitudinally elongated sclerenchyma; integument and nucellus undiverged as in modern cycads; lagenostome very small.

c. *Trigonocarpon pusillus* Brongniart.—A 3-angled ovule 12 mm. ×6 mm.; integument of three layers: outer, parenchymatous sarcotesta with numerous mucilage or resin canals, bounded externally by thick-walled epidermal cells; middle, parenchymatous, with dense cell contents; inner, sclerotesta or stony layer; relationship indefinite.

d. *Trigonocarpon parkinsoni* Brongniart.—Large seedlike structure, ovoid with 12 ribs; integument thick, differentiated into three layers: outer, parenchymatous sarcotesta, bounded by heavy-walled epidermis; middle, lacunar tissue making up the ribs; inner, sclerotesta, of cells longitudinally elongated; three major ribs show distinctly thickened intracostal dehiscence tissue in the upper one-third of their length. Nucellus similar to that found in *Pachytesta*, massive with sclerenchymatous chalazal disk, 8–12 conductive strands running longitudinally, and an outer densely colored epidermis. Casts of such seed remains are numerous throughout the coal seams.

e. *Stephanospermum akenoides* Brongniart.—An elongated ellipsoid ovule, 10 mm.×5 mm., with conspicuous crown of tissue about the micropylar end; slightly 6-angled; integument of two layers:

outer, multiple palisade; inner, longitudinally elongated sclerenchyma.

2. With the exception of *Lepidocarpon*, these forms represent the remains of orthotropous ovules, unattached to the plants which bore them, although the matrix of leaves and stems in which they were found may give some clue as to the parent plant. The nucellus is always plasmolyzed as in poorly fixed tissue for histological study. It may consist of only a single layer of cells or of a multicellular layer showing some differentiation (epidermis, conductive tissue, parenchyma). No embryos were found, and often only traces of the megagametophytes were present. This cannot be owing entirely to the delicacy of such tissues, since bud tissue and even distinctly meristematic tissue are often found in other parts of the plant remains. It is presumed that those ovules with pollen chambers intact represent an early or middle stage in the development of the ovule. Others (where the nucellus is only a thin papery layer and the pollen chamber an elongated broken beak) probably represent the discarded seed coat after the embryo has been discharged in the normal process of germination. Certain impressions of *Trigonocarpon* from Ohio seem to suggest such a stage. Where a younger stage may be definitely recognized, the petrifaction may more accurately be referred to as an ovule; where it cannot be determined with certainty, "seed remains" is more accurate than fruit or nut.

3. An environmental theory, emphasizing the conditions under which each was fossilized, is proposed to account for the close relationship between the casts found in the shales above the coal seams and the petrified ovules of the coal balls imbedded in the coal layers.

The writer wishes to express sincere appreciation to Dr. A. C. NOÉ, who furnished the material and under whose direction the work was done. Appreciation is extended also to Dr. C. J. CHAMBERLAIN for his kindly advice and suggestions.

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[*Accepted for publication June 2, 1931*]

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PINOXYLON DAKOTENSE KNOWLTON FROM THE CRETACEOUS OF THE BLACK HILLS[1]

CHARLES B. READ

(WITH TWELVE FIGURES)

Introduction

The Mesozoic strata of the Black Hills have long been famous as cycadeoid-bearing terrains, but the associated remains of Coniferae have received very little attention. A few have been described, however, and of these, *Pinoxylon dakotense* (17) is one of the most interesting. It has been the subject of comment in a number of papers dealing with the wood structure of the Coniferae, and has entered into the consideration of the antiquity of the Abietineae, although its anatomical features have never been well understood. In this paper an attempt is made to demonstrate the true nature of this wood, and to discuss its probable affinities.

The type slides are in the United States National Museum, as is the block from which the sections were cut.[2] The locality, as recorded in the manuscript catalogue of slides, is, "Above the Atlantosaurus beds 3 miles NW of Sturgis, S. D. Collected by *Lester F. Ward*, Oct. 3, 1898." In a note on the geologic occurrence, WARD states that the wood was found, "In pink and white sands overlying carbonaceous shales containing lignite" (17). Concerning the age of this horizon, he states (17):

> When I obtained it [the wood] I had no doubt of the Jurassic age of the bed in which it occurred, but Dr. KNOWLTON finds the internal structure very modern in character, scarcely distinguishable from that of *Pinus* except in the absence of fusiform rays. I hesitate, therefore, to assert that the age is certainly Jurassic.

In his "catalogue of Mesozoic and Cenozoic Plants" KNOWLTON referred *Pinoxylon dakotense* to the Lakota sandstone (Lower Creta-

[1] Submitted for publication with the permission of the Director of the United States Geological Survey.

[2] No. 30871 in the collection of types of fossil plants, United States National Museum.

ceous), and this opinion is confirmed by REESIDE.[3] RUBEY, in commenting on the horizon, states:

These "carbonaceous shales" might be Fuson instead of Lakota. According to DARTON and PAIGE's map, "Dakota" (Fall River of Russell) is improbable in this locality, but Morrison, Lakota, or Fuson crop out over wide areas. Of the three I would guess upper Lakota or sandstones in the Fuson.[4]

Description

The original diagnosis given for *Pinoxylon* is brief: "Internal structure same as in *Pinus* except in the absence of fusiform rays" (17). An examination of the types has shown that the material differs in several other respects from *Pinus*. A summary of the generic characters is as follows.

PINOXYLON KNOWLTON

Pinoxylon.—KNOWLTON, F. H., 20th Ann. Rp. U.S. Geol. Survey, pt. II. 420–422. 1900.

Protopiceoxylon.[5]—GOTHAN, W. Kungl. Svensk Vet. Handl. **42**: 32–36. 1908.

Protopiceoxylon.[5]—GOTHAN, ECKHOLD. Jahrb. Preuss. Geol. Land. **42**:489. Berlin. 1922.

ANNUAL RINGS.—Present, usually well marked.

RESIN CANALS.—Vertical canals normal; horizontal system absent or developed as a result of injury; epithelial cells thin or thick-walled, variable.

WOOD RAYS.—Uniseriate or partly biseriate, variable in size. Fusiform rays absent except in traumatic areas; pitting abietinean, that is, abundant on all walls; marginal ray cells modified into elements resembling ray tracheids, or undifferentiated. Resin abundant.

WOOD PARENCHYMA.—Absent or present; when the latter, diffuse or terminal.

TRACHEIDS.—Bordered pits radial in early wood; radial, or radial and tangential in late wood of ring. Pitting in part opposite and separate and in part alternate and contiguous.

MEDULLA.—Variable; often sclerotic.

[3] REESIDE, J. B. JR., Oral communication. 1931.

[4] RUBEY, W. W., Written communication. 1931.

[5] The explanation for this synonomy is given in another paragraph in this paper.

PINOXYLON DAKOTENSE KNOWLTON

Pinoxylon dakotense.—KNOWLTON, F. H., 20th Ann. Rp. U.S. Geol. Survey pt. II. 420–422. 1900.

ANNUAL RINGS.—Well marked, late wood forming as much as half the increment, transition usually gradual; rings variable in width.

RESIN CANALS.—Only vertical present, these chiefly small, circular to elliptical in outline, single or grouped; epithelial tissue 2–3 cells thick, of heavy-walled, highly resinous parenchyma. Traumatic passages formed as result of wounding, these observed only in vertical position.

WOOD RAYS.—Uniseriate or occasionally biseriate in part, 1–26 cells high, chiefly 4–12; cells oval to elliptical in outline as viewed in tangential section, often resinous. In radial section cells appear pitted on all walls, 3–5 small, simple (?) pits on lateral walls per crossfield; upper, lower, and terminal walls heavily pitted and slightly rugose; terminals oblique. Marginal cells variable, often thin-walled and irregular in shape, non-resinous, suggesting ray tracheids.

WOOD PARENCHYMA.—Present; terminal and in vicinity of resin passages; occasionally elsewhere.

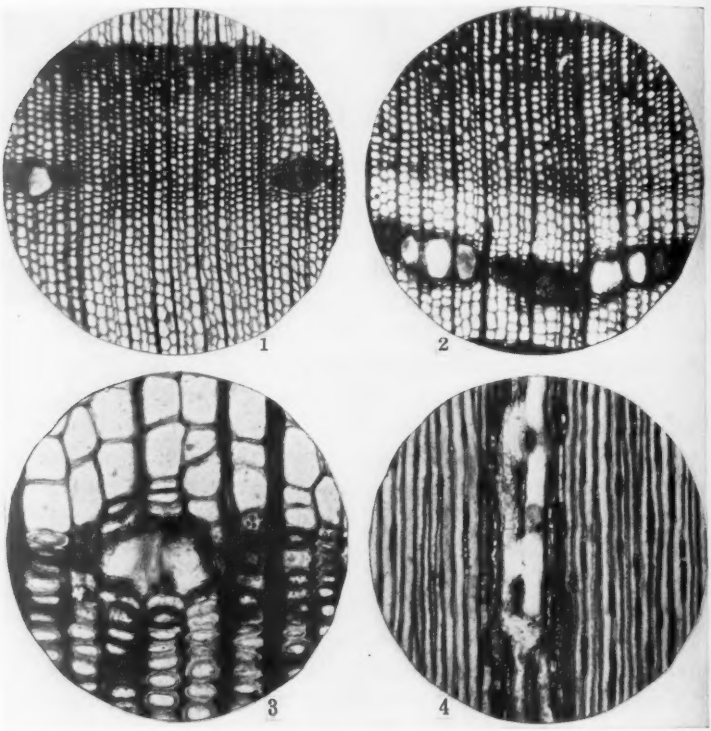
TRACHEIDS.—Pitted on radial walls in early wood; on radial and tangential walls in late wood; pits chiefly biseriate, occasionally uniseriate or triseriate; arranged in two patterns: (1) distant and if more than uniseriate, opposite; and (2) contiguous and alternate, the borders flattened. "Resin lenses" occasional.

MEDULLA.—Not observed.

Collected by *Lester F. Ward* in 1898 from a locality 3 miles northwest of Sturgis, S. D.

Figure 1 shows the general aspect of *Pinoxylon dakotense* as seen in transverse section. The annual rings are well developed, and the zone of late wood forms almost half of each increment. This is in striking contrast with the feebly developed rings usually found in Mesozoic conifers. As conspicuous elements there will be noted several resin ducts either solitary or grouped in bands of two or three. Figure 2 represents another portion of this section, showing the resin canals arranged in a series of considerable lateral extent. (In the block from which the section was cut this tangential "line" measures almost a centimeter in length.) These may be interpreted as trau-

matic ducts, and are considered by some anatomists as demonstrating the derivation of our wood from highly resinous types. In figure 3 the greater magnification shows the details of structure as seen in transverse section. The resin passages are lined with two or three

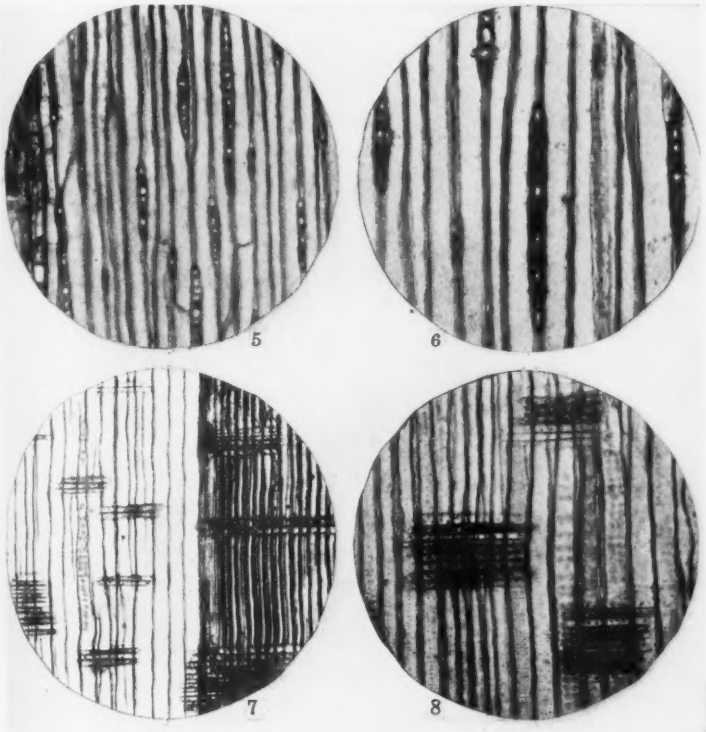


FIGS. 1–4.—Fig. 1, transverse section of wood; ×40. Fig. 2, transverse section showing traumatic resin ducts; ×40. Fig. 3, transverse section at base of ring of growth showing details of resin canal and terminal parenchyma; ×180. Fig. 4, tangential section of wood; ×30.

rows of secretory cells. In addition there are occasional resin cells on the face of the increment. Such a combination of characters is common in certain genera of the Abietineae.

An illustration of a tangential section is seen in figure 4. A resin

canal which traverses the wood vertically is prominent, but the complementary system of horizontal passages so common in the Abietineae is lacking. This feature of development of normal vertical rays without the horizontal passages is anomalous. The linear rays



FIGS. 5–8.—Fig. 5, tangential section of wood; ×70. Fig. 6, tangential section of wood; ×130. Fig. 7, radial section of wood; ×30. Fig. 8, radial section of wood; ×70.

contain many resin-filled cells, as indicated by the opaque lumens. Figures 5 and 6 show the details of the tangential section. The circular to elliptical shape of the ray cells is perhaps of specific value.

Figure 7 illustrates a radial section of *Pinoxylon dakotense* at a medium magnification. The ray cells are abundantly pitted on all walls, an abietinean characteristic. A feature of particular interest

is the peculiar pattern of the bordered pits on the radial walls of the tracheids. Gradations are to be seen, from uniseriate distant and biseriate opposite pits, of the type characteristic of the Abietineae, to uniseriate crowded and biseriate or triseriate alternate and contiguous pits similar to those which occur in the secondary wood of the Araucarineae. At the face of the ring of growth there are strands of wood parenchyma. The walls are perforated by simple pits.

Figures 8–10 present the details of the structure of the rays. The elements are solely parenchymatous, with the possible exception of empty marginal elements of irregular shape which suggest ray tracheids. The details of pitting are not well enough preserved, however, to allow a final decision. In most of the ray cells the lateral pits are readily seen. These are small, usually simple, and vary in number from two to five per cross-field. The upper, lower, and terminal walls are likewise abundantly pitted and rather rugose, a character pointed out by KNOWLTON.

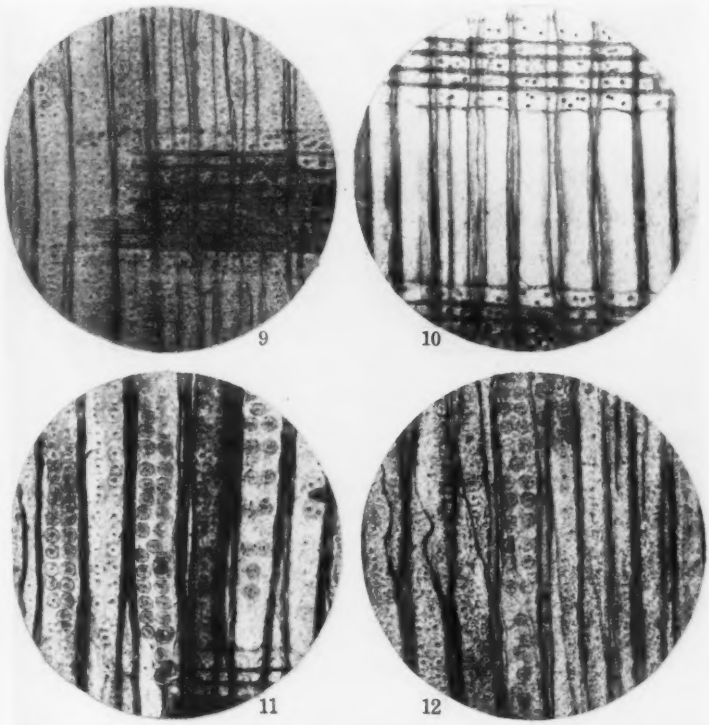
Figures 9, 11, and 12 illustrate in detail the pattern of the pitting on the radial walls of the tracheids. The occurrence of two-ranked opposite pits in close proximity to alternate and flattened pits is obvious. In this connection it is pertinent to point out that observations have indicated that alternation is most common at the extremities of the tracheids and opposition is the rule in the medial portion.

Comparison

In the foregoing description it has been shown that *Pinoxylon dakotense* is a coniferous wood characterized in general by: (1) normally developed vertical resin ducts; (2) rays of abietinean type; (3) tracheids bearing bordered pits arranged on the radial walls, partly as in modern Abietineae and partly as in existing Araucarineae; and (4) terminal, and to some extent, diffuse wood parenchyma. Among the numerous genera of Mesozoic coniferous woods there is one, *Protopiceoxylon* Gothan (**2, 6, 7**), with which *Pinoxylon* closely agrees. The best diagnosis is given by ECKHOLD (**2**):

> Tracheidtüpfel in den verschiedenen Übergangsformen, im Spätholz meist zahlreiche Tangentialtüpfel, Abietineentüpfelung vorhanden, nur normale senkrechte Harzgänge, wagerechte höchstens infolge von Verwundung, Kreuzungsfeldtüpfel klein, kein Holzparenchym, typische Quertracheiden fehlend.

From this it is seen that *Pinoxylon* differs from *Protopiceoxylon* only in the presence of "Holzparenchym." WALTON has recently described *Protopiceoxylon wordii* (**25**), in which terminal parenchyma occurs, and in addition has pointed out the suggestion of paren-



FIGS. 9–12.—Fig. 9, radial section of wood; ×130. Fig. 10, radial section showing structure of rays; ×130. Figs. 11, 12, radial sections showing details of pitting; ×130.

chyma shown in GOTHAN'S plates of *P. exstinctum* (**6, 7**). GOTHAN himself suggested that KNOWLTON'S *Pinoxylon* might be generically identical with *Protopiceoxylon* (**6, 7**), and the preceding discussion makes it appear that this is the case. In consequence, *Pinoxylon* becomes the correct generic designation for the species which have been referred to GOTHAN'S genus. A list of these is given in table I.

Pinoxylon (*Protopiceoxylon*) *salisburioides* (Krausel) (**16**) is an imperfectly known species from the Braunkohl. Its reference to *Protopiceoxylon* or *Pinoxylon* is questionable in view of the late age. The description is brief and without illustrations, so that an accurate comparison with *P. dakotense* is impossible.

Pinoxylon (*Protopiceoxylon*) *edwardsi* (Stopes) (**21**) from the Lower Greensand of Sussex, England, differs from *P. dakotense* in the occurrence of dominantly uniseriate bordered pits on the radial walls

TABLE I

SPECIES OF PINOXYLON PREVIOUSLY REFERRED TO PROTOPICEOXYLON

SPECIES OF PINOXYLON (PROTOPICEOXYLON)	HORIZON	LOCALITY
salisburioides	Braunkohl	Germany
edwardsi	Lower Greensand	England
johnseni	Lower Cretaceous-Upper Jurassic	König Karls Land
arcticum	Jurassic	Franz Josef Land
exstinctum	Jurassic	Spitzbergen
lindleii	Triassic	England

of the tracheids (these being infrequently crowded), in the lower rays, in the smaller size of the resin ducts (which are limited almost entirely to the summer wood), and in the absence of terminal parenchyma. From the description given by STOPES, this species is markedly abietinean in its composition.

Pinoxylon (*Protopiceoxylon*) *arcticum* (Seward) (**20**) likewise differs greatly from the American species. The rays are considerably higher, and opposite pitting is common. Terminal parenchyma appears to be absent. An interesting similarity is the occurrence "on the upper and lower edges of some of the rays" of "empty elements of unequal breadth which in all probability are ray tracheids" (**20**). The presence of marginal cells, striking in their resemblance to ray tracheids, has already been pointed out in *P. dakotense*.

Pinoxylon (*Protopiceoxylon exstinctum* (Gothan) (**6, 7**) is the type of the genus *Protopiceoxylon*, and is known from both König Karls Land and Spitzbergen. In the development of a distinct araucarian type of pitting in the tracheids, it closely agrees witn *P. dakotense*,

but differs in the absence of terminal parenchyma (although WALTON (**25**) has pointed out elements which suggest parenchyma on GOTHAN'S plates of this species), and in the presence of traumatic horizontal resin canals.

Pinoxylon (*Protopiceoxylon*) *wordii* (Walton) (**25**) is based on specimens from the Jurassic strata of Spitzbergen. *Pinoxylon dakotense* resembles this wood closely in the presence of terminal parenchyma and biseriate pits in the tracheids. This last named feature is not so markedly araucarian in *P. wordii* as in *P. dakotense*.

Pinoxylon (*Protopiceoxylon*) *lindleii* (Whitham) was one of the first coniferous woods to be investigated (**26, 27**). It has been referred at various times to *Peuce*, *Araucarioxylon*, *Planoxylon*, and *Protopiceoxylon* (**2, 19, 22, 26, 27**). From the several descriptions, it appears to resemble *P. dakotense* in the development of ray tracheid-like structures. In ray heights, however, and in the absence of wood parenchyma, there are features which point to specific difference.

Pinoxylon (*Protopiceoxylon*) *johnseni* (Schroeter) (**3**) differs from our wood in the lower rays, the absence of terminal parenchyma, and the typically uniseriate arrangement of the bordered pits on the walls of the tracheids. No mention is made of marginal ray tracheids.

The resemblance of *Pinoxylon dakotense* to members of the Abietineae has already been mentioned. Perhaps the most striking agreement is with *Larix*, which, however, carries a horizontal system of canals and typically fails to show araucarian pitting. With *Pseudotsuga* the same differences are manifest. (The spiral markings in the tracheids of *Pseudotsuga* are held to be features not likely to be preserved in petrifaction.) *Picea* likewise agrees in all respects save the resin canals and the pattern of the radial pits.

The absence of horizontal resin canals is unique, but does not disprove a relationship with the Abietineae. Both the rays and the wood parenchyma tend to confirm such a reference. It is in the radial pitting of the tracheids that a situation occurs which is not commonly found in the normal secondary wood of any living genus of the Coniferae.

A striking and unusual feature is the development of well marked rings of growth in this Cretaceous wood. The relationship of annual increments to climate has never been carefully analyzed, but there is

obviously a direct connection. It seems safe to point out the indication of seasonal variations of some sort during Lakota time in the Black Hills province. Whether these conditions were regional or local it is manifestly impossible to say.

Affinities

There now remains to consider the broader relationships of *Pinoxylon*. Woods with characteristics relating them to both the Abietineae and the Araucarineae have long been known, but owing to differences of opinion concerning the criteria which afford accurate indices to the true affinities of such woods, interpretations have been various and conflicting. KRAUS (**15**), in one of the earliest classifications, concluded that the radial pitting of the tracheids provided the most accurate guide in separating abietinean from araucarian forms. Woods with opposite and separate bordered pits he placed in the Araucarineae. GOTHAN (**5**), on the other hand, considered the nature of the rays to be fundamental. Woods with heavily pitted rays he regarded as abietinean, and woods with unpitted, thin-walled ray cells he regarded as araucarian. The tracheid pitting was considered to be of minor importance.

In America considerable taxonomic value has been attached to the bars of Sanio which are claimed to be present in the secondary wood of all living Coniferae with the exception of the Araucarineae (**4, 8**). This feature, in connection with the pit pattern in the tracheids, has been used in one of the latest attempts at separation of the tribes (**23**). SEWARD (**20**), THOMPSON (**24**), and others have questioned the universal application of these structures in distinguishing putative Araucarineae from Abietineae. BAILEY (**1**) has added a word of caution as to their interpretation. It must be admitted that bars of Sanio are of slight practical value in the study of silicified woods where such delicate structures are not likely to be preserved.

Accepting the hypothesis of Cordaitalean derivation of the conifers, there are two divergent views concerning the relationships of the several tribes. The opinion held by many paleobotanists and anatomists is that the Araucarineae represent either the primitive group of the Coniferae or else constitute a distinct line. In opposition to this is the view held by certain investigators who consider the

Abietineae as ancestral stock and the Araucarineae as derivatives. Since these theories bear on the position of *Pinoxylon*, certain of their salient features are here discussed.

According to JEFFREY (**11, 13**) and his associates (**23**), the Abietineae are the oldest of the modern conifers. In support of this view, two "canons of comparative anatomy" are cited: (1) ancestral characters which are absent in mature vegetative axes may be found in foliar organs, reproductive axes, and first annual rings of rapidly growing shoots; and (2) wounding recalls ancestral conditions (**13**). The fundamental bases of the arguments in favor of the primitiveness of the abietineans are these canons. In addition, a sequence of fossil forms has been introduced, one interpretation (**23**) of which favors the derivation of the Araucarineae from the Abietineae. *Woodworthia* is regarded as the Triassic ancestor of the modern Abietineae, characterized as it is by araucarian wood and persistent brachyblasts (**1**). From this old stock there developed gradually the type of wood structure found in the Cretaceous *Pityoxyla*. After this development the Araucarineae are supposed to have branched off; and by a process of gradual elimination of resin cells, resin canals, pitted rays, and a substitution of alternate for opposite bordered pits, the modern type of araucarian wood was derived. One of the most obvious weaknesses of this theory is the failure of its adherents to produce concrete evidence of the links between *Woodworthia* and *Pityoxylon*. *Pinoxylon* has been suggested as a probable intermediate by JEFFREY and CHRYSLER (**14**), who state:

> Without considering the evidence for the existence of Abietineae at earlier geologic periods than the Tertiary, furnished by impressions of the foliage, etc., there are now definite records based on internal structure, which carry the group far into the past. KNOWLTON has recently described an abietineous wood from the Jurassic beds of the Black Hills of Dakota which he calls *Pinoxylon dakotense*.

In a more recent paper in support of the antiquity of the Abietineae TORREY (**23**) states:

> The earliest known woods of araucarian affinity were discovered by GOTHAN in Jurassic deposits of Spitzbergen. . . . . The most primitive of these woods is *Protopiceoxylon* (an example of most unhappy nomenclature). It is a wood in which the degenerative process is just beginning.

Since it has been demonstrated that *Pinoxylon* and *Protopiceoxylon* are synonymous, we are obliged to regard the preceding statements as contradictory. TORREY'S paper is the most recent comprehensive discussion pointing to the antiquity of the Abietineae, and apparently is in accord with JEFFREY'S ideas; consequently we may infer that the exponents of abietinean primitiveness regard the latter opinion as correct.

Opposition to this theory is found in the papers of GOTHAN (**5–7**), SCOTT (**18**), THOMPSON (**24**), and many others who point out (1) the resemblances between the Araucarineae and the Cordaitales; (2) the fact that wood of the *Araucarioxylon* type, and hence the Araucarineae, antedates records of abietinean forms in the geologic sequence; (3) the evidence of transitional fossil forms; and (4) certain recapitulatory, vestigial, and traumatic phenomena held to indicate Cordaitalean ancestry for the Araucarineae. Of these, only the arguments relating to the geologic evidence of the antiquity of the araucarians and to the interpretation of the transitional forms are within the realm of this paper.

Wood of the *Dadoxylon* or *Araucarioxylon* type is well known from the Paleozoic to the Recent. In pre-Mesozoic strata most of this material is referable to the Cordaitales. Foliage shoots and fertile axes such as *Walchia*, *Voltiza*, *Ulmannia*, and *Gomphostrobus* furnish additional evidence which is held by some investigators to demonstrate the presence of araucarian forms in the Permian. Wood of the *Araucarioxylon* type and impressions of leafy twigs and strobili of types bearing an external resemblance to the araucarians are known from the Triassic. In the Jurassic and later strata there are abundant records of the Araucarineae. As regards the Abietineae, all records of Paleozoic representatives have been vigorously disputed and disproved. Likewise the nature of the Triassic *Woodworthia* (**23**) has been questioned. Thus there seem to be no known Abietineae which can compare in antiquity with forms attributed to the Araucarineae.

Among the transitional forms, the advocates of the theory of araucarian primitiveness point out that the earliest (*Woodworthia*) bears a much closer resemblance to *Araucarioxylon* than do the later forms (*Araucariopitys*, etc.) which resemble the Abietineae more closely. Resin canals are absent in the former but present in the latter. The

rays of the latter are abietinean while those of *Woodworthia* are araucarian. *Araucariopitys* and related forms do not show such a markedly araucarian pattern of the tracheid pitting as does *Woodworthia*. These points are regarded as fundamental objections to the abietinean derivation of the Araucarineae. It is interesting to note that both theories are based on the same evidence, but differ fundamentally in the interpretations of it.

Considering now the position of *Pinoxylon* in these hypothetical lines of phylesis, the advocates of abietinean antiquity place it in a primitive position in the Araucarineae and regard it as being immediately derived from the resinous Abietineae. On the other hand, the supporters of araucarian primitiveness regard *Pinoxylon* as a form preceding the *Pityoxyla* and differing chiefly in the absence of horizontal resin canals.

This discussion makes it apparent that links of vital necessity are lacking in the demonstration of the evolution of the Coniferae. In consequence, it does not seem wise to accept these theories as more than working hypotheses. The weight of the evidence indicates abietinean affinities for *Pinoxylon*, but the writer does not care to commit himself finally on this at the present time. Instead he prefers to consider *Pinoxylon* as occupying an extremely uncertain position within the Coniferae, and to reserve any expression of positive opinion until additional material which may connect the now known forms can be secured and studied.

Summary

1. *Pinoxylon dakotense* Knowlton is a coniferous wood from the Lakota sandstone of the Black Hills, South Dakota.

2. It has been related to *Pinus*, but differs (1) in the absence of horizontal resin ducts; (2) in the presence of wood parenchyma; and (3) in the partly araucarian character of the pits on the radial walls of the tracheids.

3. The rays are abietinean, and show marginal elements which resemble tracheids markedly.

4. *Protopiceoxylon* Gothan is generically identical with *Pinoxylon* Knowlton, and consequently is synonymous.

5. The rings of growth indicate considerable seasonal variation in climate.

6. This wood, showing as it does features which relate it to both the Abietineae and the Araucarineae, cannot definitely be assigned to either tribe with impunity, owing to our present incomplete knowledge of the early history of the Coniferae.

UNITED STATES GEOLOGICAL SURVEY
WASHINGTON, D. C.

[*Accepted for publication August 23, 1931*]

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NATURE AND DEVELOPMENT OF THE TRACHEIDS OF THE OPHIOGLOSSACEAE

GASPER A. LOUGHRIDGE

(WITH TWENTY-FOUR FIGURES)

Introduction

The object of this study has been the tracing of the development of the tracheids of the Ophioglossaceae. These tracheids are unusual for ferns, in that they bear on their walls distinct bordered pits resembling those characteristic of many of the higher plants, instead of the scalariform markings characteristic of the other Filicales.

The three genera of the Ophioglossaceae are all represented in the survey. *Helminthostachys*, the monotypic genus from the East Indies, was available in the department. *Ophioglossum*, the type genus, was represented by *O. vulgatum* L., our native terrestrial species, and by *O. pendulum* L., an epiphytic form from Java. *Botrychium* was represented by *B. obliquum* Muhl. and *B. ternatum* (Thunb.) Sw. of the division Septridium; *B. simplex* E. Hitchcock, *B. ramosum* (Roth) Aschers, and *B. lunaria* (L.) Sw. of the division Eubotrychium; and *B. virginianum* (L.) Sw. of the division Osmundopteris, our most common native species.

Fresh material was fixed by three methods: (1) JEFFREY'S (6) corrosive sublimate and picric acid; (2) alcohol formalin; and (3) alcohol, formalin, and acetic acid. All material was treated with a 10 per cent solution of hydrofluoric acid for a week or ten days to remove any trace of silicates before imbedding and sectioning. Material was imbedded in celloidin when serial sections were not desired; when serial sections were desired the paraffin method described by ZIRKLE (8) was used to greater advantage than the method of infiltration with chloroform.

Four methods of staining were used with sections of buds: erythrosin and crystal violet (JACKSON 5) was used when very young lignified elements were to be differentiated; otherwise combinations of safranin with crystal violet, Ehrlich's haematoxylin, or Haidenhain's haematoxylin were used. In later work a combination of fast

green and safranin gave excellent differentiation of the three regions of the wall, the middle lamella standing out clearly from the secondary cellulose thickening. Celloidin sections of the stem were stained with combinations of safranin with Ehrlich's haematoxylin, Haidenhain's haematoxylin, and fast green.

Drawings were made with the aid of the camera lucida except for the diagrams of the buds, which were made by the aid of the Promi projection apparatus.

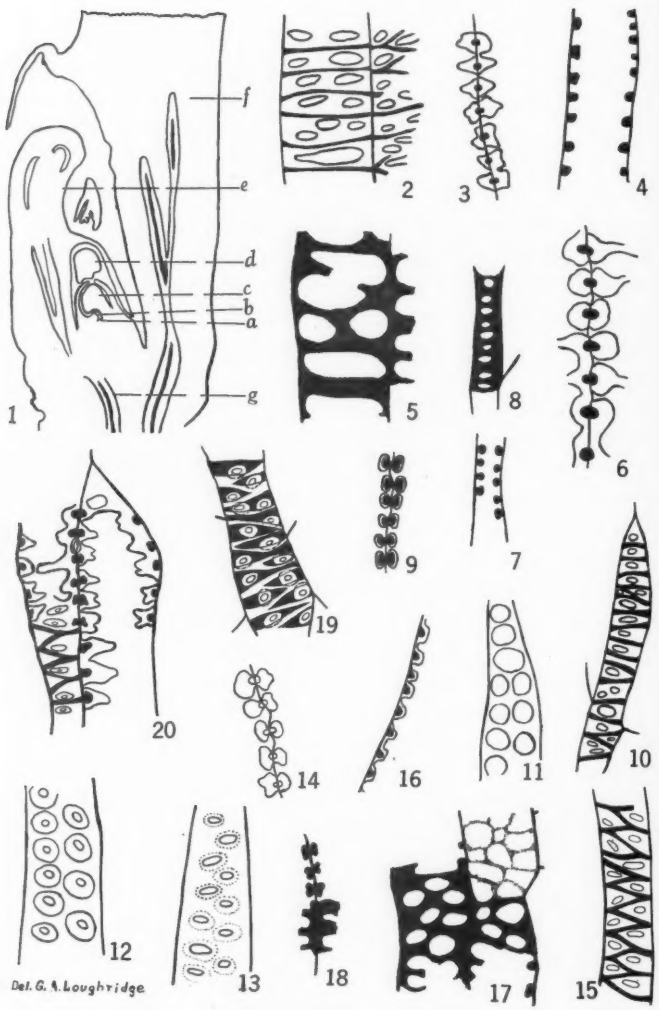
Early work on the Ophioglossaceae has been summarized ably by CAMPBELL (2) and BOWER (1). Little has been done on the nature of the tracheids. The nature of the pit-closing membrane was discussed by WRIGHT (7) in a paper in which the nature of the tracheid walls of *Ophioglossum vulgatum*, *Botrychium obliquum*, and *Helminthostachys zeylanica* was described as a more or less incidental observation.

Nature of tracheids

The terminal bud in most species consists of a series of leaves of different ages, one of which reaches maturity each year. A longitudinal section of the bud of *Botrychium virginianum* (fig. 1) shows portions of four such immature leaves and the basal portion of the petiole of the five-year old leaf, which was mature at the time of the collection of the material. The apical region of the stem is to be noted between the bases of the two youngest leaves. Similar conditions are to be observed in the buds of the other members of the family. Such buds and stem tips lend themselves particularly well to a study of the development of the tracheids.

The tracheids which make up the greater part of the xylem of the stem of the Ophioglossaceae differ from those which are characteristic of the pteridophytes. In most ferns the tracheids exhibit either spiral or scalariform markings on their walls. In this group, however, the spiral and scalariform elements are confined to the protoxylem of the stem and portions of the vascular strands of leaves, the mature tracheids of the metaxylem and secondary xylem bearing on their walls elongated or rounded pits.

The wall of the tracheids throughout the entire group consists of three regions, the middle lamella of cellulose, a secondary thickening of cellulose, and a tertiary thickening of lignin.



FIGS. 1–20.—Fig. 1, *Botrychium virginianum:* diagram of longitudinal section of bud, collected in the fall of 1927: *a*, apical region of stem; *b*, 1-year old leaf; *c*, 2-year old leaf; *d*, 3-year old leaf; *e*, 4-year old leaf; *f*, petiole of mature leaf; *g*, central cylinder of stem; xylem indicated in black. Fig. 2, *Ophioglossum vulgatum:* surface view of

In *Ophioglossum vulgatum* the surface view of a tracheid from a root trace shows the middle lamella with a secondary thickening of cellulose appearing as black bars over which may be seen the tertiary lignification forming uniseriate or multiseriate pits (fig. 2). By a shift of focus, a portion of the wall of the same cell may be seen in section (fig. 3) which more clearly demonstrates the position of the tertiary lignification over the secondary cellulose bars. In *Botrychium lunaria* a similar condition is demonstrated. In sections of the bud, such as are shown in figure 1, maturation of the tracheids may be traced from the earliest differentiation of the elongated cells with the primary wall only to the beginning of the formation of the secondary cellulose scalariform markings or pittings (as are seen in section in figure 4 or in surface view in figure 5) and to the mature condition where the secondary cellulose wall is completely covered by the tertiary layer of lignin (fig. 6). *B. ramosum* shows the same type of wall as is found in the tracheids of *B. lunaria*. In a surface view of the cell, secondary thickenings of cellulose appear through the tertiary thickening of lignin (fig. 15), and a shift of focus shows the same cell in section with its cellulose secondary wall surrounded inwardly by the lignified tertiary thickening (fig. 16).

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tracheid from root trace; secondary thickening indicated in black, tertiary in white. Fig. 3, longitudinal section of wall of same tracheid as shown in fig. 2. Fig. 4, *B. lunaria:* longitudinal section of tracheid as found near apex of stem in longitudinal section of bud; secondary thickening in black. Fig. 5, surface view of same cell as shown in fig. 4. Fig. 6, longitudinal section of portion of tracheid from older region of same bud. Fig. 7, *B. virginianum:* longitudinal section of tracheid as found near apex of stem of young plant, showing primary and secondary wall. Fig. 8, surface view of same cell as shown in fig. 7. Fig. 9, longitudinal section of mature tracheid from same bud, showing tertiary thickening. Fig. 10, surface view of same cell as shown in fig. 9. Fig. 11, *Helminthostachys zeylanica:* surface view of tracheid from stem apex, showing secondary thickening forming pits. Fig. 12, surface view of older tracheid, showing lignification of borders of pits. Fig. 13, surface view of mature tracheid with tertiary lignification covering the wall. Fig. 14, longitudinal section of wall of similar mature tracheid showing two thickenings and primary wall of cell. Fig. 15, *B. ramosum:* surface view of tracheid of stem as shown in longitudinal section of bud. Fig. 16, longitudinal section of portion of same tracheid as shown in fig. 15. Fig. 17, *B. obliquum:* surface view of tracheids near apex of bud cut in longitudinal section, showing development of secondary wall. Fig. 18, a portion of wall of one of same cells as seen in section. Fig. 19, a more mature tracheid from apex of same stem, showing secondary thickenings in black and tertiary lignifications in white as borders to pits and as bars. Fig. 20, mature tracheids from apex of same bud as seen in section and surface views. Fig. 1, ×4.5; figs. 2–20, ×810.

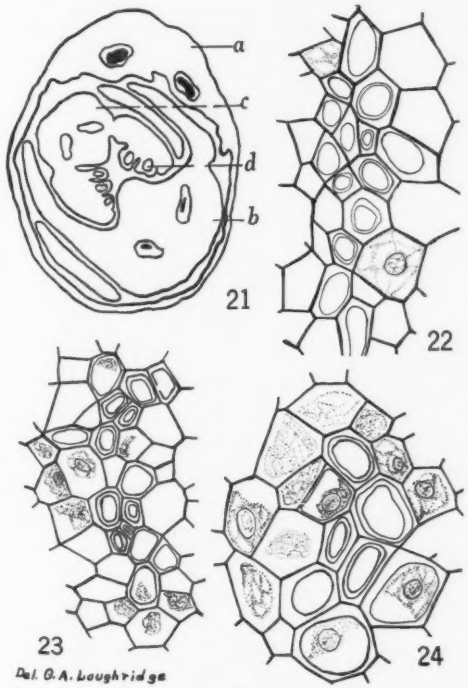
Botrychium virginianum resembles the other members of the genus in respect to the development of the tracheids. In longitudinal sections of the bud of a young plant, tracheids near the apical region show only the secondary thickening of cellulose (figs. 7, 8). Tracing back along the central cylinder, tracheids are found in which the cellulose wall is covered by the tertiary wall of lignin (as seen in section in figure 9 or in surface view in figure 10). Transverse sections of a young bud show the same conditions in the vascular strands of the various leaves (figs. 22–24), in the cells of which all stages from the primary to the mature tertiary condition of thickenings are to be seen. In *B. obliquum* the first differentiation of the tracheid wall takes the form of scalariform cellulose thickenings laid down on the primary wall and tending to form bordered pits (figs. 17, 18). This differentiation is followed by a lignification of the rim of the pits and the development of tertiary bars of lignin on the margin of the cellulose thickening (fig. 19). These tertiary bars soon become confluent and completely cover the cellulose thickenings, which may show through the lignin in surface view or appear surrounded by the lignin when the wall is seen in section (fig. 20).

Helminthostachys zeylanica exhibits the same character of development of the tracheids as is found in the other members of the Ophioglossaceae. Here the secondary wall of cellulose is laid down, giving rise to a pitted wall (fig. 11). These pits soon become rounded out by lignification along their margins (fig. 12) which spreads over the secondary thickening as a tertiary wall of lignin completely concealing the secondary wall in surface view (fig. 13), although the latter may still be distinguished in sections of the tracheid wall (fig. 14).

Rate of differentiation of tracheids

It was found that differentiation and maturation of the tracheids takes place in a short space back of the apical region in the stem; mature elements appear within a few cells of the region of their first differentiation. This is probably due to the extremely slow elongation of the stems of these plants. In the leaves, however, the progressive differentiation may be traced more easily. In transverse sections of the bud of very young plants of *Botrychium virginianum*, the petioles of several leaves may be distinguished, varying

in age by one year each as it proceeds inward (fig. 21). The vascular strands appear early in the development of the leaf, and mature tracheids may be distinguished as much as two years before the leaf is to reach maturity. The number of mature tracheids steadily in-



FIGS. 21–24.—Fig. 21, *Botrychium virginianum:* diagram of transverse section from near apex of bud of young plant collected June, 1929: *a*, base of mature leaf; *b*, base of leaf which should have reached maturity in 1930; *c*, blade of leaf which should have reached maturity in 1931; *d*, archesporial tissue of leaf; ×14. Fig. 22, detail of xylem from vascular strand of leaf *a* at level 80 μ below that shown in fig. 21; ×490. Fig. 23, detail of xylem from vascular bundle of leaf *b* at level 80 μ below that shown in fig. 21; ×490. Fig. 24, detail of xylem from vascular strand of leaf *c* at level 80 μ below that shown in fig. 21; ×810.

creases from the time of their first appearance until maturation of the leaf (figs. 22–24). The same conditions are to be observed in sections of older buds of *B. virginianum* and other members of this family.

This earlier development of the leaf is not confined to the vascular strand, but is also evident in respect to the segregation of the archesporial tissue. In cutting a bud of a plant in its third year of development, archesporial tissue was observed in a leaf which would have reached maturity two years later (fig. 21). All of the cells of this archesporial tissue were in the metaphase stage before formation of the spore mother cells.

Discussion

Tertiary thickenings are not uncommon in the higher plants. They have been described in such plants as *Pseudotsuga*, *Torreya*, *Magnolia*, and *Tilia*. FROST (4) reports having found tertiary thickenings in 41 out of 260 species examined. Such thickenings are generally considered to be an indication of great specialization and high evolutionary advancement in a given series.

Tertiary thickenings as found in the higher plants consist of spiral bars of lignin laid down on a secondary thickening of like material. In this respect they differ from those described for the Ophioglossaceae, in which the tertiary thickening is a layer of lignin completely covering the secondary cellulose thickening.

It was hoped in the beginning that such a study might throw some light on the evolutionary sequence within the Ophioglossaceae, but there is so little difference in the nature of the tracheid development that the observations serve only to bind the group more closely as a unit.

The slowness in differentiation of the tracheids has been noted in the leaf in contrast to the short region of differentiation in the stem. This may be attributed to the more rapid growth of the leaf, making possible the extension of the region over which the differentiation is taking place, as is characteristic of conservative organs of plants; whereas the stem, being less conservative, crowds the transition region and complete differentiation is to be seen in a short interval of space.

The presence of tertiary thickenings may be considered as evidence confirming the conclusions, which other investigators have reached on the basis of embryology and gross morphology, that the Ophioglossaceae represent a highly specialized group among the pter-

idophytes, and that they may be considered as the living remnants of an old evolutionary line.

The early differentiation of the sporogenous tissue in the young bud may throw some light on the age at which *Botrychium virginianum* reaches maturity. This plant would have produced its first spores during its fifth year of development.

Summary

1. The buds in the Ophioglossaceae are made up of a series of three to five leaves, one of which reaches maturity each year.

2. The rate of differentiation of the tissue in the stem appears rapid, the transition region being short.

3. Differentiation and maturation of the leaf trace of the Ophioglossaceae is a slow process.

4. Lignification and maturation of the tracheids begins in the leaf as early as four years before the leaf reaches maturity.

5. Archesporial tissue is differentiated in *Botrychium virginianum* two years before the leaf reaches maturity.

6. The tracheid walls in the Ophioglossaceae are made up of three distinct regions: the middle lamella or primary wall; a secondary thickening of cellulose forming bars or scalariform markings on the wall; and a tertiary thickening of lignin which covers the secondary thickening completely and gives rise to the characteristic bordered pits.

7. Secondary thickening differs from that of the spermatophytes in respect to the substance present.

8. Tertiary thickening of the Ophioglossaceae differs from that of the spermatophytes in that it almost completely covers the wall, and gives rise to the bordered pits; that of the latter consists of spiral markings.

9. The great similarity in nature and in development of the tracheid walls of the members of this group is an indication of the close affinity of the members.

The writer wishes to acknowledge his indebtedness to Professor M. A. Chrysler for suggesting this problem and for valuable advice and criticism throughout the investigation. Acknowledgment is also

due Dr. L. C. PETRY of Cornell University for material of *Ophioglossum pendulum*, and Dr. H. S. HOLDEN of the University of Manchester for material of *Botrychium lunaria*.

GOODLAND, IND.

[*Accepted for publication August 24, 1931*]

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MEIOSIS IN THE GENUS HYPERICUM[1]

CARL SHERMAN HOAR AND EDWIN JACOB HAERTL

(WITH PLATE I)

As recorded in a previous discussion of the classification of *Hypericum* (HOAR 4), the species *H. punctatum* Lam. was considered separately because of the peculiar arrangement of the chromosomes at the time of diakinesis and their subsequent behavior. The present article deals with the meiotic behavior, chromosome counts, etc., of other species of *Hypericum* found growing, for the most part, in New England and other portions of northeastern United States. For this purpose the writers are in possession of sixteen species, varieties, and known hybrids. The methods used in this study are much the same as those employed for *H. punctatum* (4).

The first species considered is the one most commonly found in New England, namely, *H. perforatum* L. This species is found almost everywhere in open fields, pastures, beside roads, etc.; and strange as it may seem, it is the one species not native to the region. It was probably introduced from Europe. The early development of the pollen mother cells up through diakinesis does not appear peculiar. No such chain formation as found in *H. punctatum* is apparent. Indeed no such chain formation has, so far, been found in any other species of the genus. At diakinesis the spireme appears broken, and the homologous chromosomes seem to pair in the usual manner. This also is characteristic of all other species examined, with the exception of *H. punctatum*. The chromosome count, as reported by NIELSON (5), is apparently sixteen. However, owing to the excessive clumping of the chromosomes, the count is not easily ascertained. In the second (homeotypic) division the haploid count is also difficult to determine, and, as shown by figures 1 and 2, is by no means always the same. Figures 7 and 8 seem to explain this discrepancy, since lagging chromosomes are common. So far as could be determined no extra nuclei nor pollen grains are formed, and ap-

[1] Contributions from the Department of Biology, Williams College, Williamstown, Massachusetts.

parently the lagging chromosomes either eventually reach the plate or degenerate. This peculiarity in the behavior of the chromosomes may account for the fact that there are so many morphologically sterile pollen grains. Probably the true haploid count is sixteen, but even if it happened to be eighteen it would not preclude the possibility of *H. perforatum* being a tetraploid form, since there are many species of *Hypericum* with either eight or nine chromosomes as the haploid number. It does not seem unlikely that this increase in the number of chromosomes came about through hybridization, but there is no evidence of recent crossing. Figures 3–5 show various stages in the development of the female gametophyte. They illustrate the fact that this development in *Hypericum* is of the usual type. Figure 3 shows the chain of four megaspores with the upper three ready to abort. Figure 4 illustrates the binucleate stage of the developing embryo sac, and in figure 5 the 8-nucleate stage is shown with the nuclei in position for fertilization and future development. Although no stage showing fertilization was observed, yet embryos were easily found, and many of them were approaching maturity. On the other hand, aborted megasporangia were not uncommon.

The species *H. adpressum* Bart. is found growing on moist, sandy shores chiefly near the coast from Massachusetts southward. The material used in this study was collected on Cape Cod. Its haploid count, as shown in figure 12, proved to be nine. Diakinesis shows paired chromosomes in the usual manner. No morphological sterility of pollen grains appears, and the species seems normal. Its variety *spongiosum* (*H. adpressum* var. *spongiosum* Robinson) was also collected from the same locality. It is taller than the regular species and the stem has a spongy, thickened base. It also has a haploid count of nine (fig. 16), and its chromosomes behave in a normal manner. It apparently grades into the regular species in passing from the very wet spots (even open water) back to the dry land. In both *H. adpressum* and in its variety it will be noted that chromosomes are larger than in most other shrubby species with a count of nine.

Several exotic species, often cultivated as ornamental plants, were collected at the Arnold Arboretum. All these appear to have a haploid count of nine, although in one or two cases the chromosomes

have the tendency to clump and thus to make difficult the determination of the count. *H. lobocarpum* Gattinger is a shrub, native in North Carolina and Tennessee according to REHDER (6). Its cytology seems to be perfectly regular. *H. arnoldianum* Rehd. (fig. 18) is considered to be a hybrid between *H. galoides* Lam. and *H. lobocarpum*. Probably its parents are very compatible, since no irregularity in chromosome behavior nor morphological sterility of pollen was evident. *H. dawsonianum* Rehd., a hybrid between *H. lobocarpum* and *H. prolificum*, which looks like the latter but has a many-flowered inflorescence and 3–5 capsules, also appears normal from the cytological standpoint. *H. aureum* Bartr., a shrub with handsome flowers, is a native of South Carolina, Tennessee, and southward. It, like the other members of the group, has a haploid count of nine and the normal behavior of chromosomes. *H. nudiflorum* Michx. (fig. 6), likewise a small southern shrub, grows from North Carolina to Florida and westward to Alabama. Here, and also in *H. kalmianum* L., which in contrast to the preceding species is a hardy northern shrub ranging north of New England from Quebec westward to Michigan, the haploid count is the usual nine and the behavior of the chromosomes is normal.

H. ellipticum Hook. (fig. 11), another species with a haploid count of nine, is a native of New England. It is herbaceous, growing in wet spots and having bright yellow, rather large flowers which sometimes show a reddish or purplish color. The specimens used in this study were collected in a wet springy spot near the road in Worthington, Mass. Many examples of complete pollen development were found and nothing irregular was observed with regard to the chromosomes or pollen. Many stages in embryo sacs and embryo development were also noted. Figure 17 illustrates the female gametophyte in the 4-celled stage.

The next group differs from most species of the genus in having relatively few (5–12) stamens. They are all small herbs, either annual or perennial. *H. mutilum* L. is easy to identify since the leaves have a broad, blunt appearance and the plants grow in rather dense clusters. GRAY'S Manual (3) states that the leaves are "ovate to narrowly oblong, obtuse, partly clasping, and 5-nerved." Those used in this study were collected in Williamstown and in Acton, Mass. Material for practically all stages of development of both

pollen grains and embryo sacs, as well as embryos, was available and the behavior throughout appears normal. Here the haploid count is clearly eight. Another member of this group, *H. boreale* (Britton) Bicknell, is also a low herb, but is not tufted as is *H. mutilum*, and the leaves are "elliptical, rounded at the tip, sessile, 3–20 mm. long, and 3–5 nerved" (3). It is characteristically found growing near bogs and margins of ponds. Those studied were collected at the edge of Perch Pond in Pownal, Vt. Here again the cytology is regular and the haploid count is eight. *H. canadense* L., with "leaves 1–3 nerved, linear to linear oblanceolate, rounded at tip, narrowed to the sessile or subpetiolate base" (3), is in appearance much like *H. boreale*. It may grow in wet or dry places. That studied was collected in a wet, sandy, road gutter in Worthington, Mass., a spot which would be dry in a dry season. Its haploid count (fig. 15) proved to be eight and regular. Figure 9 shows the embryo sac with the eight chromosomes not yet arranged. *H. majus* (Gray) Britton also appears more like the latter two species than like *H. mutilum*, but its stems are more erect than *H. boreale* and distinctly stouter than *H. canadense*. It also often has a more tufted growth than either. Its leaves, according to GRAY, are "chiefly 5–7 nerved at the rounded or subcordate, sessile or clasping base." On the whole, they are distinct in appearance and larger than the two previous species. The material was collected on the wet, sandy shore of Lake Oneota in Pittsfield, Mass., and in a dry open field in Williamstown, Mass. Here again the chromosome behavior is regular and the haploid count proved to be eight. In figure 19 a young embryo is illustrated.

H. gentianoides (L.) BSP, also called *Sarothra gentianoides* L. and thus placed in a separate genus by BRITTON and BROWN (1), proved of special interest. It grows in distinctly sandy, dry soil, and does not attract attention as a member of the genus *Hypericum* except for its minute, yellow flowers. Its stems and branches, as GRAY states, are "rigid, erect, and bushy," and its leaves are "minute, awl-shaped scales." The plant has a somewhat grasslike appearance. The material studied was collected at the Beaver Brook Reservation in Waverley, and in Acton, Mass. In the former place it grew in a sandy pit and in the latter it grew in the hard, arid soil of an old cart path. The pollen sacs contain but few, twelve or more, pollen

mother cells, and these, as shown in figure 14, are two or three times as large as those typical of the earlier species recorded. Its haploid chromosome count (fig. 14) proved to be the unusual number of twelve. No irregularity of chromosome behavior or of pollen sterility was noted. Most of the stages of embryo sac development were observed, and likewise many stages were seen of embryo development up to maturity. In several cases masses of tissue were seen at both ends of the embryo sac. These, when young, were of about the same size and led the senior writer to believe that polyembryony occurred. After careful study of more fully developed embryos, however, it became evident, as shown in figure 10, that the second group of cells came from the proliferation of the antipodal cells. It had somewhat the appearance of a young embryo, but was less regular and more like a multinucleate mass, although in some cases cell walls between the nuclei were in evidence. At first no such proliferation was observed in any other species, but later it was seen in *H. punctatum*, indicating that it may be found elsewhere among the members of the genus. Such proliferation is not an uncommon happening, especially in the monocotyledons, the Ranunculaceae, and the Compositae. As COULTER and CHAMBERLAIN (2) state: "the character of the active antipodals among the more primitive Monocotyledons and in the Ranunculaceae may be regarded as indicating a primitive condition of the nutritive tissue in the female gametophyte of Angiosperms: and antipodals of many of the Compositae are organized into an aggressive haustorium which can only be regarded as a specialized organ."

Whether *H. gentianoides* should be regarded as a separate genus or not is difficult to determine; but the entirely different chromosome count, and the difference in general aspect of the plant lead one to wonder whether perhaps *Sarothra* is not a better classification than is *Hypericum*. The frequent occurrence of antipodal proliferation, while at first thought to separate this species from others of the genus, appears not to, since it was found also in *H. punctatum;* however, it seems to be much less frequent in the latter.

H. virginianum L. is classified by BRITTON and BROWN (1) as *Triadenum virginianum* (L.) Roff. It is a perennial, stoloniferous, marsh plant with flesh-colored or purplish flowers. The leaves are larger than those in most other species of *Hypericum*, being "closely

sessile or clasping by a broad base, oblong or ovate, and very obtuse. . . . . The entire plant frequently has a pink or crimson tone." The specimens used in this work were collected at the very edge of Lake Oneota near Pittsfield, Mass. In figure 13 a pollen mother cell is illustrated. It will be noted that its size is larger than most of those of other species but smaller than those found in *H. gentianoides*, and the haploid count is clearly nineteen. The pollen sac is much larger than that of *H. gentianoides* and there are many more pollen mother cells in each sac. A striking fact is that many of the pollen grains abort and yet no chromosome aberrations were noted. One peculiarity is that the pollen mother cells show many cytoplasmic connections (fig. 23), the meaning of which is not clear. It is also true that the pollen grains often germinate in the anther, a peculiarity not noted elsewhere in the genus. The female gametophytic development was not difficult to follow, nor was that of the embryo, and a few stages of each are illustrated. Figure 22 shows the second division in the formation of the megaspores. In figure 20 one can clearly discern the chain of four megaspores, the upper three being small and functionless, and the lower one being large, round, and full of cytoplasm. Figure 21 gives an excellent idea of the developing embryo with the stalk portion and the embryo proper at the end.

The unusual chromosome count and the distinctive outward appearance, as well as other factors, make one wonder whether BRITTON and BROWN (1) are not correct in taking the plant out of the genus *Hypericum*. Likewise the frequent morphological sterility of the pollen, the intercellular connections of the pollen mother cells, and the germination of the pollen while still in the anther are unusual points of interest.

Summary

1. The unusual chain formation already observed (4) at the time of diakinesis in *Hypericum punctatum* apparently does not occur in any other species described in this article.

2. In every form studied the chromosomes seem to pair in the usual manner at diakinesis.

3. *H. perforatum* appears to have a haploid count of sixteen. During meiotic division its chromosomes often tend to lag. At ma-

turity many of its pollen grains are morphologically sterile and aborted. Because of its chromosome count it is apparently a tetraploid form, and because of its chromosome behavior and abundant pollen sterility it may be a natural hybrid.

4. The species *H. adpressum* and its variety *spongiosum*, as well as *H. lobocarpum*, *H. aureum*, *H. nudiflorum*, and *H. kalmianum*, appear to have a haploid chromosome count of nine and to be regular in chromosome behavior. The chromosomes in *H. adpressum* and its variety *spongiosum* are distinctly larger than those found in the other forms just mentioned.

5. *H. arnoldianum* and *H. dawsonianum*, which are recognized as hybrids, have a haploid count of nine and apparently come from compatible parents, since their chromosome behavior is regular and no morphological sterility is present.

6. *H. ellipticum*, *H. mutilum*, *H. boreale*, *H. majus*, and *H. canadense* all have a haploid chromosome count of eight, and the chromosome behavior is normal.

7. *H. gentianoides*, called by BRITTON and BROWN *Sarothra gentianoides*, is in many ways distinct from the other species studied. The haploid chromosome count is twelve.

8. *H. virginianum*, classified by BRITTON and BROWN as *Triadenum virginianum*, is also distinct. The haploid chromosome count is nineteen.

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[*Accepted for publication October 7, 1931*]

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EXPLANATION OF PLATE I

Magnification of figures is ×2540 unless otherwise specified.

FIG. 1.—*H. perforatum:* pollen mother cell at time of second division, showing chromosome count of 16.

FIG. 2.—*H. perforatum:* pollen mother cell during second division, showing chromosome count of 13.

FIG. 3.—*H. perforatum:* chain of four megaspores showing upper three small and abortive and lower one larger and ready for further division; ×1735.

FIG. 4.—*H. perforatum:* chain of four megaspores with lower one already divided to form 2-celled stage; ×1200.

FIG. 5.—*H. perforatum:* female gametophyte in 8-celled stage with nuclei already arranged and ready for entrance of pollen tube; ×1735.

FIG. 6.—*H. nudiflorum:* pollen mother cell at time of first division, showing haploid count of nine.

FIG. 7.—*H. perforatum:* pollen mother cell showing anaphase of first division with several lagging chromosomes.

FIG. 8.—*H. perforatum:* similar to fig. 7.

FIG. 9.—*H. canadense:* female gametophyte at 8-celled stage but with nuclei not yet arranged; ×800.

FIG. 10.—*H. gentianoides:* early stage in formation of embryo—embryo at right side of endospermic membrane, proliferating antipodal cells at left; ×182.

FIG. 11.—*H. ellipticum:* pollen mother cell at time of first division, showing haploid chromosome count of nine.

FIG. 12.—*H. adpressum:* pollen mother cell at time of first division, showing haploid chromosome count of nine (note that chromosomes are larger than those in figs. 6 and 18).

FIG. 13.—*H. virginianum:* pollen mother cell at time of first division, showing haploid count of 19.

FIG. 14.—*H. gentianoides:* pollen mother cell at time of first division, showing haploid count of 12.

FIG. 15.—*H. canadense:* pollen mother cell at time of first division, showing haploid count of eight.

FIG. 16.—*H. adpressum* var. *spongiosum:* pollen mother cell at time of first division, showing haploid count of nine (note that chromosomes are large as in *H. adpressum*).

FIG. 17.—*H. ellipticum:* female gametophyte at 4-celled stage; ×800.

FIG. 18.—*H. arnoldianum:* pollen mother cell at time of first division, showing haploid count of nine.

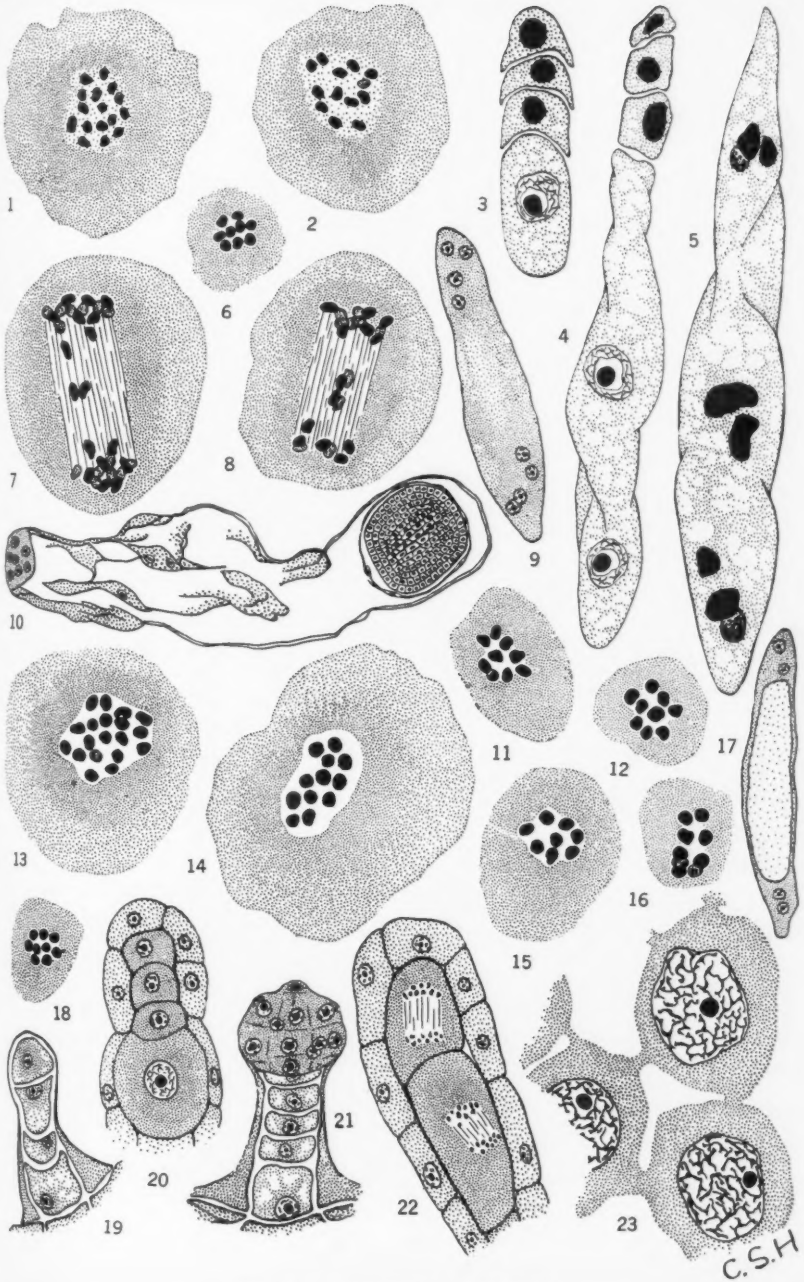
FIG. 19.—*H. majus:* young embryo; ×535.

FIG. 20.—*H. virginianum:* chain of four megaspores with upper three small and abortive; ×1200.

FIG. 21.—*H. virginianum:* young embryo further developed than in the case of embryo of *H. majus* shown in fig. 19; ×600.

FIG. 22.—*H. virginianum:* megaspore mother cell undergoing second or homeotypic division; ×1735.

FIG. 23.—*H. virginianum:* pollen mother cells showing numerous intercellular connections; ×1735.



HOAR & HAERTL on MEIOSIS

CARPEL DEHISCENCE IN FIRMIANA SIMPLEX

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 432

TSU-KIANG YEN

(WITH NINE FIGURES)

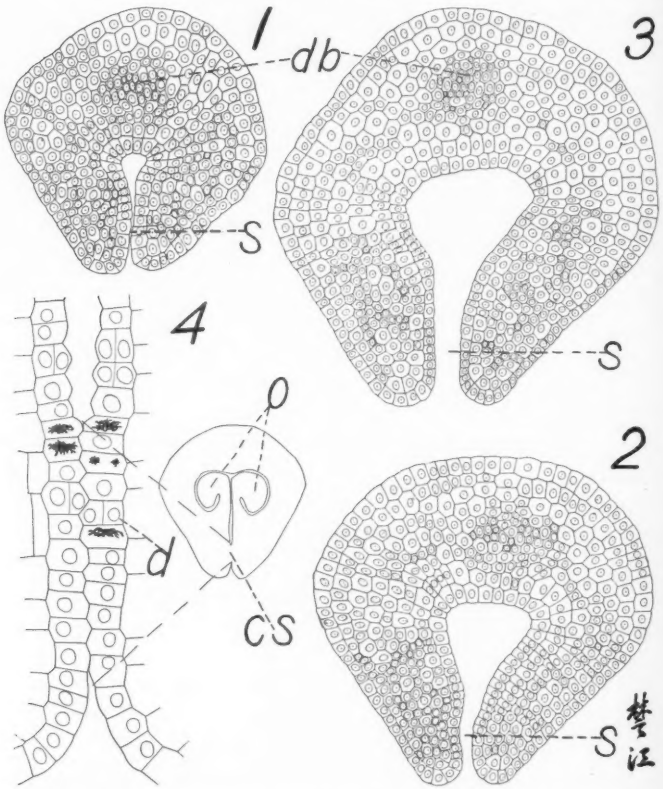
There have been a number of recent investigations dealing with the development of the carpels of various groups of plants. GRÉGOIRE (3) found that the edges of the carpel forming the ventral suture in the Ranunculaceae approach each other very closely, so that no space remains between them, the cells of the epidermis of either edge often being papillate and fitted between each other. In the Papilionaceae, however, there is no distinct line between the two edges of the carpel at any time. There is a continuous mass of parenchymatous cells where the suture might be, but no indication of a line of coalescence. The inner epidermis of the carpel is continuous over the ovules but shows no connection with the outer epidermis.

BUGNON (1) has reviewed GRÉGOIRE'S work, and states that in the young flower of *Lathyrus vernus* Bernardi (*Orobus vernus* L.), *Trifolium pratense* L., and *Lupinus perennis* L., the young carpels are open as in the Ranunculaceae; and later the two edges of the carpel become united, as previously stated by PAYER (5) and GOEBEL (2).

The material for this study was collected at the National Central University, Nanking, China, and was brought to the Hull Botanical Laboratory, University of Chicago, for investigation.

The follicle of *Firmiana simplex* (L.) W. P. Wight is of interest in that, in the early stages of its development, the carpel edges are distinct and separate; later they are firmly united; and still later they are again widely separated. In the young carpel, 0.21 mm. long, the two inner rims nearly meet each other (fig. 1), but there is a distinct narrow slit between them. At this stage the marginal or placental bundles have scarcely started to differentiate; the midrib or dorsal bundle has become slightly differentiated; but there is no

trace of epidermal cuticle. The five carpels of a common androgynophore diverge and begin to grow in length and circumference (6). At this early stage there is no stigma developed. The growth



FIGS. 1–4.—Fig. 1, cross-section through young carpel 0.21 mm. in length, showing suture of carpel almost closed: *db*, procambium of dorsal carpellary vascular bundle; *s*, suture. Fig. 2, cross-section through young carpel 0.27 mm. long, showing space of suture wider than in fig. 1. ×234. Fig. 3, cross-section showing suture in its full width when carpel is 0.37 mm. long: *db*, procambium of dorsal carpellary vascular bundle. ×234. Fig. 4, cross-section through carpel 0.57 mm. long, showing final coalescence of the two rims of carpel and tangential cell dividing of the epidermis which is the starting point of development of the additional new sutural tissue: *d*, epidermal cell showing tangential dividing; *cs*, coalescence of carpel. ×550.

of the young flower is very rapid. Every carpel is hoodlike or half-crescent shaped in outline. The basal portion of the carpel is much larger and broader than the tip. These carpels are surrounded completely by the stamens. The sutures of the carpels face each other around a common center.

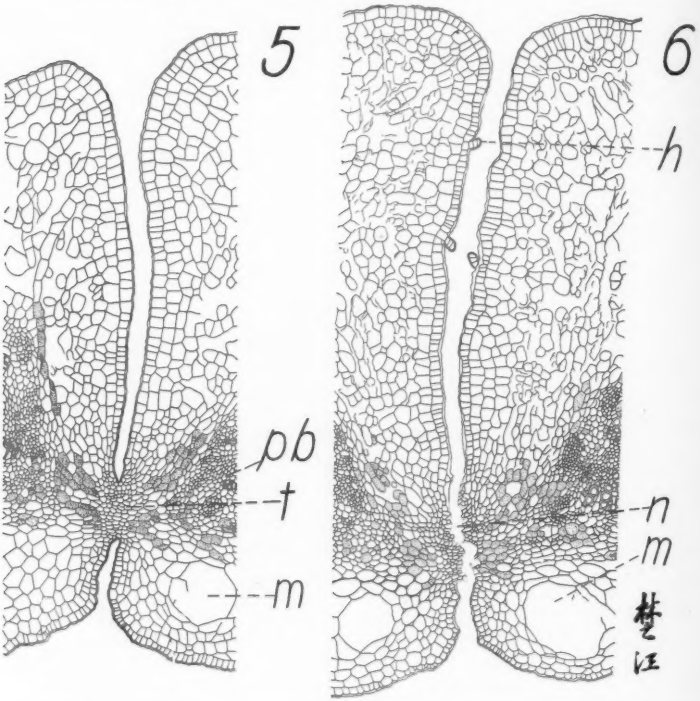
There is great variation in the suture of the young carpel. After the earliest stages, the suture continues to widen (fig. 2), reaching its full width when the carpel is 0.32 mm. in length (fig. 3). Since the cells near the margins of the suture and those of the placental bundles continue to enlarge and actively divide, the margins of the carpel approach each other. The gap thus becomes successively narrower, until the two margins are brought into close contact. A cross-sectional view (fig. 4) of a carpel 0.57 mm. in length shows that the suture is being closed. The epidermal cells of these margins which are in contact continue to divide tangentially to the line of the suture, as shown in figure 4. Eventually all the epidermal cells along the entire length of the suture divide actively, thus effecting a complete coalescence of the margins of the carpel, which appears as a complete cylinder. Except near the inner and outer surfaces of the carpel, all traces of the former space between the margins are obliterated, and it is impossible to determine definitely those cells which previously formed a part of the epidermis.

Cell division continues throughout the entire basal portion of the carpel, resulting in its appreciable growth and enlargement. When the carpel is about 1.6 cm. in length, the cells near what had been the old line of the suture, both on the interior and exterior surfaces, begin to separate, although the remaining cells of the carpel continue to divide actively until the full length of the carpel, which is 7–10 cm., is attained. At this stage the carpel is still closed, but active cell division ceases (fig. 5).

Following this, a mechanical rupturing of the tissue, approximately along the old line of the suture, results in a new suture, the line of final dehiscence of the carpel (fig. 6). The broken ends of the cell walls show that the first suture had been completely sealed and obliterated, and that the cells which had filled in were less likely to be pulled apart or ruptured than those adjacent to them. Final dehiscence is a purely mechanical breaking of cell walls. These broken

cell walls shrink until only a dark brown line on either margin of the carpel is visible; and soon, by the elongation of the surrounding cells, shrunken tissue is more or less overgrown (fig. 7).

The writer (4) has previously stated that "the pistil of *F. simplex* consists of five distinct carpels, coalesced only at the upper stylar



FIGS. 5, 6.—Fig. 5, cross-section through portion of suture of carpel, showing well developed new sutural tissue; after this stage the carpel breaks open: *m*, mucilaginous canal; *pb*, placental vascular bundle; *t*, new tissue. Fig. 6, cross-section through portion of suture of one portion of carpel 7 cm. in length, showing mechanical breaking of carpel through sutural tissue; dotted cells contain tannin: *h*, capitate hair; *n*, new suture. ×76.

and lower basal regions, though when young they appear to be undiverged throughout the length of the carpel." A more careful observation of this coalescence reveals the fact that, as has been men-

tioned, each young carpel is a hoodlike scale, or half-crescent shaped in outline. The upper portions of the carpels are more closely in contact than are their bases. This upper portion, which has grown together, elongates into a slender column, the style. During the development and elongation of the stylar region, both the epidermal cells and those near the inner surface of each primordium, which are in contact, divide actively. The majority of the cell divisions are tangential to the surface of the carpel wall, and thus the five distinct

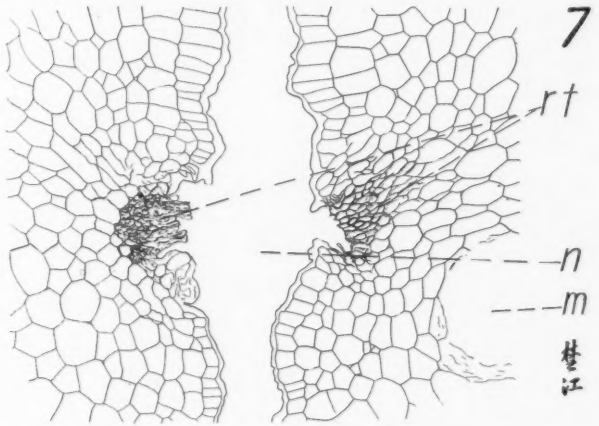


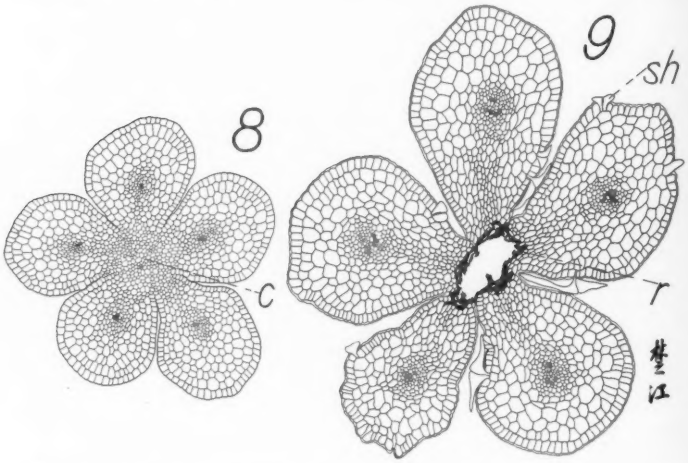
FIG. 7.—Cross-section of mature carpel showing broken cells overgrown by elongation of surrounding cells: *n*, new suture; *m*, mucilaginous canal; *rt*, remnant of new tissue. ×149.

primordia become coalesced and form a single style. The coalescence of the style begins at a very young stage of the flower, when it is a little less than 1 mm. long, and is completed by the time the primordium is 1.3 mm. in length. A cross-section through the mid-stylar region of a young flower shows a complete coalescence of the carpels, this region appearing as though never having consisted of separate parts (fig. 8).

In the young flower primordia the five tips never join closely together at their very ends. Each tip of a carpel gives rise to a portion of the stigma, and this portion is on the top and adaxial surface of the carpel. The stigma is a compound structure, but these five

different portions of the stigma never coalesce completely; there are five distinct areas clearly seen as composing the stigma, even in its later stages.

The coalescence of the carpels is relatively ephemeral. After pollination the stigma begins to wither and the lower portions of the carpels to separate. During the separation the later developed cells in the center of the style begin to degenerate; the style breaks off;



FIGS. 8, 9.—Fig. 8, cross-section through middle of stylar region of young flower bud 1.0 mm. long, showing coalescence of five carpels at their common center: *c*, coalesced tissue. Fig. 9, same as fig. 8 when flower is 4 mm. long, showing degeneration of later developed tissue in center of stylar region: *r*, remnant of degenerated tissue. ×113.

and cell walls adjacent to the line of rupturing become highly suberized (fig. 9). After this degeneration the five carpels completely separate from one another at their upper portions. In the meantime there is a basipetal growth of the lower portion of each follicle. The basal portion grows and elongates; and a slender pedicel-like stalk extending from each of the five follicles to the androgynophore is the result of this basipetal growth. The separation of the carpels is completed at this time. The follicle is more or less fusiform. Brown stellate hairs densely cover its outer surface, and there are glandular

capitate hairs on the inner surface of the carpel. The carpel grows both in length and circumference.

According to evolutionary progression, the Ranunculaceae are generally considered to be primitive; the Papilionaceae are somewhat less advanced than the Sterculiaceae, although both are placed near the middle of the angiosperms. So far as the development of the suture of the carpel is concerned, the majority of the Papilionaceae are the same as the Ranunculaceae. At first there is a suture in the young carpel and the margins coalesce at the later stage (**1, 3**). This characteristic is shared by *Firmiana simplex*. Its suture does not coalesce entirely across the entire width of the carpel wall, however, but, as has been mentioned, there remains a small gap near the inner and outer surfaces of the carpel. It may be that the carpel of *F. simplex* represents a condition between a completely closed carpel and an open one.

Moreover, the syncarpous condition is considered advanced and the apocarpous character is considered rather primitive. In *Firmiana simplex* the syncarpous condition is ephemeral and present for only a short time during the period of pollination, as during that period the five distinct carpels are joined throughout their common stylar region. This may indicate also that the pistil is an intermediate stage between the apocarpous and the syncarpous conditions.

Summary

1. The young carpel of *Firmiana simplex* is closed at first, then opens widely, later closes intimately, and again becomes widely opened.

2. Coalescence of the two rims of a single carpel is by means of close approximation, cell division, and cell enlargement.

3. Development of additional sutural tissue is brought about by the activity of the cells at either margin of the carpel, which meet and then divide tangentially to the suture.

4. Coalescence of the carpel margins also is due more or less to the enlargement and division of the cells of the two placental bundles.

5. No trace of former suture can be observed in the tissue after coalescence.

6. The carpels open by mechanical breaking. This breaking ruptures individual cells, indicating that the former opening has been completely eliminated.

7. Coalescence of the stylar regions takes place before pollination, and later the entire style withers and is broken off.

8. The stigma is derived from the top and adaxial surface of the sporophyll.

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[*Accepted for publication November 2, 1931*]

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* The English spelling of the writer's last name had been NYI, and according to Mandarin, YEN is the standard spelling.

STUDIES IN THE GENUS BIDENS.
X. FAMILY COMPOSITAE

CONTRIBUTIONS FROM THE HULL BOTANICAL LABORATORY 433

EARL EDWARD SHERFF

At the present time there are 208 known species in the genus *Bidens* L. These fall into no fewer than fourteen sections. Several of these sections have been recognized for nearly a century, or since the work of AUGUST DECANDOLLE and THOMAS NUTTALL. The majority, however, have been overlooked by workers upon the genus. This was doubtless due in part to the fact that a number were monotypic and in part to the fact that it seemed simpler for the time being to force all unique or bizarre species into the already existing sections.

In my recently completed monograph of *Bidens*, the individual species have been grouped into their respective sections and these have been treated somewhat in detail. Since, however, the monograph in question may not be published for a considerable period of time, it appears wise to present herewith a more or less synoptical survey of the sections there employed:

Sect. I. CAMPYLOTHECA (Cass.) Nutt., Trans. Amer. Phil. Soc. ser. II, **7**:368. 1841 (*pro genere*, Cass. *in* Dict. Sc. Nat. **51**:475. 1827); *Adenolepis* Less., Linnaea **6**:510. 1831 (*pro genere*); *Adenolepis* (Less.)O. Hoffm. *in* Engler & Prantl Pflanzenf. 4^{v}:245. 1894 (*pro sect. Bidentis*).

Demum plerumque fruticosae, saepissime glaberrimae, suci odore carotae plus minusve similes. Capitula saepius numerosa, radiata. Achaenia recta vel torta, saepius biaristata aristis plerumque retrorsum hamosis. Plantae insularum Oceani Pacifici.-Type, *B. micrantha* Gaud. A large group consisting of 48 species. Except for *B. cosmoides* (Gray) Sherff, all species native to the Hawaiian and Marquesan Islands are referable to this section.

Sect. II. **Degeneria,** sect. nov.[1]

[1] Named for Professor OTTO DEGENER, the well known authority on the flora of the Hawaiian Islands.

Genitalia praesertim stylo longissimo valde exserta.-Type, *B. cosmoides* (Gray) Sherff. Monotypic.

Sect. III. **Neurophyllum,** sect. nov.

Herbae perennes, procumbentes, foliis crassioribus, perspicue nervatis.-Type, *B. clarendonensis* Britt. Monotypic.

Sect. IV. **Clomtonia,** sect. nov.[2]

Frutices, foliis oblongis, acuminatis, etc. Cum characteribus typi.-Type, *B. monticola* Poepp. & Endlich. Monotypic.

Sect. V. GREENMANIA Sherff, BOT. GAZ. **88**:297. 1929.

Herbae Americae tropicae perennes, plerumque scandentes, caulibus saepe 5-10 m. longis; capitulis numerosis, normaliter radiatis; achaeniis elongatis, valde obcompressis vel omnino planis, lateribus parallelis et saepissime valde setosis, apice plerumque biaristatis aristis saepius longis nunc retrorsum hamosis nunc calvis.-Type, *B. rubifolia* H.B.K. A group of ten species, among them *B. squarrosa* H.B.K., *B. reptans* L., *B. shrevei* Britt., and *B. speciosa* Gardn.

Sect. VI. **Selvorngea,** sect. nov.[3]

Herbae perennes, glabrae; foliis sessilibus, decussatis, rigidis, oblanceolato-oblongis, serratis, etc. Cum characteribus typi.-Type, *B. graveolens* Mart. Monotypic.

Sect. VII. **Fulsotsia,** sect. nov.[4]

Caulis glaber fere nudus, foliis 3-4 jugis, parvis, sessilibus, integris, linearibus. Cum characteribus typi.-Type, *B. fistulosa* Schz. Bip. *ex* Bak. *in* Mart. Monotypic.

Sect. VIII. **Heterodonta** (Nutt.) comb. nov.; *pro sect.? Diodontae* Nutt., Trans. Amer. Phil. Soc. ser. II, **7**:361. 1841; sect. *Hederodonta* Nutt. *ex* Walp. (*generis Diatontae* Nutt. *ex* Walp.) Repert. **2**:615. 1843.

Plantae boreali-americanae, foliis plerumque simplicibus, capitulis discoideis vel subradiatis et cylindricis vel ellipsoidalibus, achaeniis planis lineari-cuneatis.-Type, *B. bidentoides* (Nutt.) Britt. Section consisting of two species, the other one being *B. eatonii* Fern.

Sect. IX. **Meduseae** (Nutt.) comb. nov.; *pro sect. Diodontae* Nutt., Trans. Amer. Phil. Soc. ser. II, **7**:360. 1841; *Diodonta* Nutt. (*sed*

[2] Name anagrammatic for *monticola*.

[3] Name anagrammatic for *graveolens*.

[4] Name anagrammatic for *fistulosa*.

syn. Coreopsis aurea Ait. *et syn. Diodonta bidentoides* Nutt. *excludenda sunt) loc. cit.; pro sect. Diatontae* Nutt. *ex* Walp. Repert. **2**:615. 1843; *Diatonta* Nutt. *ex* Walp. (*exclud. syn. Coreopsidem auream* Ait.) *loc. cit.* 614. *Diadonta* Nutt. *ex* Walp. *loc. cit.* **6**:164. 1846; *pro subsect. sectionis Eucoreopsidis* Pfeiffer Nomencl. Bot. **1**: 1085. 1874 (*non vere* Torr. & Gr.).

Plantae boreali-americanae; foliis plerumque pinnatis raro indivisis vel bipinnatis; capitulis radiatis luteis; achaeniis planis nunc lineari-cuneatis nunc cuneato-obovatis saepe crasso-marginatis et plus minusve tuberculatis, exaristatis vel biaristatis aristis saepius antrorsum hamosis.-Type, *B. polylepis* Blake. The other four species of this section are: *B. aristosa* (Michx.) Britt., *B. coronata* (L.) Britt., *B. mitis* (Michx.) Sherff, and *B. oerstediana* (Benth. *ex* Oerst.) Sherff.

Sect. X. PLATYCARPAEA DC. Prodr. **5**:594. 1836.

Folia plerumque simplicia vel pinnatim 3-7-partita (raro 2-3-pinnatisecta); achaeniis ovalibus vel obovato-cuneiformibus, obcompresso-planis vel apicem versus tetragonis.-Type, or at least first cited species, *B. tripartita* L. Section includes twelve species, among them being *B. cernua* L., *B. laevis* (L.)B.S.P., *B. radiata* Thuill., and *B. connata* Muhl.

Sect. XI. PSILOCARPAEA DC. Prodr. **5**:596. 1836.

Plantae habitu valde diversae, nunc annuae nunc perennes, herbae vel frutices; foliis simplicibus vel (etiam valde) decompositis; capitulis discoideis vel radiatis, nunc minimis nunc maximis; achaeniis plerumque plus minusve linearibus, planis vel tetragonis, apice muticis vel aristatis.-Type species not indicated by DE CANDOLLE. *B. fruticosa* Forst., cited first by DECANDOLLE, unknown both to him and to me. *B. decolorata* H.B.K., the next species cited, reduces to *B. aurea* (Ait.) Sherff (*B. heterophylla* Ort.), which species may therefore serve as the section type. The numerous species referred here, 114 in all, display much diversity. Future studies may indicate the advisability of splitting this section into several smaller groups.

Sect. XII. **Steppia** (Schz. Bip. *in* Walp.) comb. nov.; *pro sect. Coreopsidis*, Schz. Bip. *in* Walp. Repert. **6**:163. 1846.

Folia dentibus apicaliter setigeris saepius dentata; floribus tubu-

losis ad medium saepius tumido-articulatis; achaeniis plerumque biaristatis aristis antrorsum hispidis.-Type, *B. chaetodonta* Sherff. Consists of ten species, all African.

Sect. XIII. **Lesperthema** sect. nov.[5]

Involucri bracteae interiores basaliter vel etiam usque ad medium connatae. Achaenia exteriora marginibus perspicue incrassata.-Type, *B. phelloptera* Sherff. Monotypic.

Sect. XIV. **Ebussa,** sect. nov.[6]

Involucri bracteae interiores basaliter vel etiam usque ad medium connatae. Achaenia praecocia, clavato-linearia, exalata, apice plus minusve incrassato-capitata vel crassiusculo-anulata.-Type, *B. praecox* Sherff. Monotypic.

SECTIONES EXCLUSAE VEL REDUCTAE

Sect. DISCOPODA DC. (Prodr. **5**:604. 1836) = *Cosmos* Cav., sect. **Discopoda** (DC.) comb. nov.

Sect. HYDROCARPAEA A. Gray (Synopt. Fl. N. Amer. **1**[II]:298. 1884) = *Megalodonta* Greene, Pittonia **4**:270. 1901.

Sect. ADENOLEPIS (Less.) O. Hoffm. *in* Engler & Prantl (Pflanzenf. **4**[V]:245. 1894) = sect. *Campylotheca supra* (*qu. vide*).

Bidens magnidisca Degener & Sherff, sp. nov.—Herba erecta, perennis, fruticosa, glabra, caule tetragona, verisimiliter 2-3 dm. alta. Folia opposita, petiolata petiolis tenuibus usque ad 9 cm. longis, petiolo adjecto usque ad 2 dm. longa, acriter serrata, nunc indivisa, ovata vel ovato-lanceolata, basi (saepe oblique) late cuneata vel rotundata vel truncato-subcordata, apice acuta vel breviter acuminata, usque ad circ. 4.5 cm. lata; nunc pinnatim 3-5-partita, foliolis ovatis vel oblongo-lanceolatis, lateralibus basi valde obliquis et saepe (praecipue superioribus) decurrentibus, plerumque 1-3.5 cm. latis. Capitula irregulariter paniculata, pedicellata pedicellis glaberrimis saepius 1-2-bracteatis plerumque 1-3.5 cm. longis, radiata, pansa ad anthesin circ. 2 vel vix 2.5 cm. lata, 0.8-1.5 cm. alta.

[5] Name anagrammatic for that of *Thelesperma*, which genus is strongly suggested by the interior involucral bracts, these being connate below (as are also those in Sect. XIV).

[6] Name anagrammatic in honor of Dr. WALTER BUSSE, collector of the type, the name *Bussea* having already been used (*pro genere*) by HARMS (Engler Bot. Jahrb. **33**:159. 1902) in another connection.

Involucrum interius primum (pro capitulo juveni) late cylindricum vel turbinato-globosum, glaberrimo-subnitidum et supra clausum, exterius patens vel reflexum; demum bracteis exterioribus (6–8) saepe irregulariter positis, glabris, ovatis vel linearibus vel late oblongis, apicem obtusum versus saepe latioribus, plerumque tantum 1.5-3 rarius 5 mm. longis; interioribus oblongo-lanceolatis plerumque 5-7 mm. longis. Flores ligulati 6–8, non perspicui, flavidi, ligula cuneato-lineares, apice acriter (saepe profunde atque irregulariter) 3–4-dentati, tantum 6–9 mm. longi et 1.5–3 mm. lati. Flores disci circ. 30–45, aurantiaci, limbo acriter profundeque 5-lobati, deorsum sensim angustati, stylis antherisque exsertis paleas lineares ac flores ligulatos superantibus. Achaenia plana, lineari-oblonga, utrinque moderate attenuata, aegre torta, glabra, brunneo-nigra, valde mediano-nervata, unaquaque facie circ. 4-sulcata, corpore 8–15 mm. longa et 1–2 mm. lata, apice ipso exaristata sed infra apicem saepe irregulariter 1–2-aristata aristis brevibus validis plus minusve calvis ex achaeniorum marginibus (alis) desinentibus manifeste productis.

Specimens examined: *Otto Degener, Kwan Kee Park,* and *F. Kruse* 4080, much localized on sunny, grassy, shrubby slope, western ridge of Waipapau Valley just within forest reserve, Hauula, Isl. Oahu, Hawaiian Isls., Oct. 11, 1931 (4 type sheets, Herb. Field Mus.: cotypes, Herb. Berl.; Herb. Brit. Mus.; Herb. Deless.; Herb. Gray; Herb. Kew; Herb. Missouri Bot. Gard.; Herb. Mus. Vienna; Herb. N.Y. Bot. Gard; Herb. Par.; Herb. U.S. Nat.; Herb. Univ. Vienna).

BIDENS SANDVICENSIS **imminuta** Degener & Sherff var. nov.—Planta ± 1 m. alta, multo ramosa ramis gracillimis. Folia pinnatim 5-partita, foliolis infimis terminalibusque saepe 3-partitis, segmentis plerumque lineari-lanceolatis saepius tantum 3–6 mm. latis et tantum 1–2.5 cm. longis. Achaenia marginaliter basim versus atque apicem versus moderate erecto-setosa, saepe 1–2-aristata aristis retrorsum hamosis usque ad 1 mm. longis.

Specimens examined: *Otto Degener, K. K. Park,* and *K. Kwon* 4092, alt. 1000 ft., grassy, shrubby plateau, narrow middle Waialae Ridge, Isl. Oahu, Hawaiian Isls., Nov. 14, 1931 (type, Herb. Field Mus., 2 sheets: cotypes, Herb. Berl.; Herb. Brit. Mus.; Herb. Boiss.; Herb. Gray; Herb. Kew; Herb. Missouri Bot. Gard.; Herb. Par.; Herb. U.S. Nat.).

Bidens fecunda Degener & Sherff sp. nov.—Fruticosa, erecta, glabra, ± 1 m. alta, ramis tetragonis. Folia opposita, petiolata petiolis

tenuibus 1–6 cm. longis, petiolo adjecto 6–15 cm. longa, pinnata; majora 5-partita, foliolis lanceolatis vel ovato-lanceolatis, acriter serratis vel paucis undulato-integris, apice acutis vel acuminatis, membranaceis, inferioribus tenuiter petiolulatis; minora saepius 3-partita foliolis lateralibus saepe sessilibus, aliter similia. Capitula plerumque numerosissima, plus minusve paniculato-corymbosa, tenuiter pedicellata pedicellis glabratis, pansa ad anthesin 1.5–2 cm. lata et circ. 6–7 mm. alta. Involucri bracteae exteriores circ. 5 vel 6, tenuiter lineari-oblongae, sparsim hispidae et ciliatae, apice obtusae, circ. 2.5–3 mm. longae, quam interiores anguste oblongae apicaliter pubescentes dimidio breviores. Flores ligulati 4 vel 5, flavi, ligula elliptico-oblongi vel oblanceolato-obovati, apice denticulati vel raro inciso-lobulati, 1–1.3 cm. longi. Paleae lineares, superne saepius attenuatae ac demum coloratae, usque ad 9 mm. longae, achaeniis maturis multo superatae. Achaenia pauca (plerumque 8–12), parce patentia, tenuissime oblongo-linearia, valde obcompressa vel interdum tetragona, nigra, faciebus 4-sulcata (4 faciebus 2-sulcatis) glabra, marginibus glabra vel sparsim erecto-setosa, corpore longiora demum 1–1.3 cm. longa et circ. 0.5–0.7 mm. lata, sub apice (rarius ad apicem) plus minusve erecto-setosa saepe 1–2-(raro 3-) aristata aristis acriter retrorsumque hamosis usque ad 1 mm. longis.

Specimens examined: *Otto Degener* and *Kwan Kee Park* 4095, near dry, partly shaded stream bed, first large side valley on south of Makua Valley, Isl. Oahu, Sept. 7, 1931 (Herb. Berl.; Herb. Field Mus.; Herb. Kew); *iidem et William Bush* 4096, on dry cliffs and less often on grassy slopes, narrow northeast gully in Ohikilolo Valley, Isl. Oahu, Nov. 29, 1931 (Herb. Berl.; Herb. Field Mus.; Herb. Gray; Herb. Missouri Bot. Gard.); *iidem* 4098, on cliffs and less often on grassy and shrubby slopes, deep, precipitous gully on north central side of Kahanahaiki Valley, Isl. Oahu, Nov. 28, 1931 (type, Herb. Field Mus., 4 sheets: cotypes, Herb. Berl; Herb. Boiss.; Herb. Brit.; Herb. Univ. Calif.; Herb. Gray; Herb. Missouri Bot. Gard.; Herb. Munich; Herb. Mus. Vienna; Herb. N.Y. Bot. Gard.; Herb. Par.; Herb. U.S. Nat.; Herb. Univ. Vienna); *iidem* 4105, rare on moderately dry, grassy slope, south crest of prominent side gully on southeast side of Keawaula Valley and directly north of Kahanahaiki Valley, Isl. Oahu, Nov. 28, 1931 (Herb. Field Mus.; Herb. Gray); *Degener, Park,* and *Kwon* 4108, dry, grassy ledges and slopes, southern slope of Kahanahaiki Valley, Isl. Oahu, Nov. 1, 1931 (Herb. Berl.; Herb. Boiss.; Herb. Brit.; Herb. Univ. Calif.; Herb. Field Mus., 2 sheets; Herb.

Gray; Herb. Kew; Herb. Missouri Bot. Gard.; Herb. Munich; Herb. Mus. Vienna; Herb. N.Y. Bot. Gard.; Herb. Par.).

I am indebted to Professor OTTO DEGENER for having given this interesting species particular note in the field and for having assembled a large assortment of specimens for my study. Besides the specimens cited here, there were collected numerous others of *Bidens torta* Sherff (growing within 20 feet of *B. fecunda*), also several which were clearly hybrids between the two species. These hybrids resemble *B. torta* in having the achenes spirally more or less twisted, although the twisting is much less regular than in *B. torta*. In other respects the resemblance to *B. fecunda* is much stronger.

COREOPSIS ASPERATA Hutch. & Dalz. Fl. West Trop. Afr. **2**:141–143. 1931.—Herba perennis, verisimiliter 1–2 m. alta, erecta, ramosa, caule ramisque subtetragonis, glabris. Folia inferiora non visa, superiora breviter petiolata petiolis planis latissimis basaliter connatis ±1 cm. longis, petiolo adjecto 6–11 cm. longa, pallida, membranacea, faciebus glaberrima, pinnatim 3–5-partita, foliolis lanceolatis acriter dentatis vel subincisis, ciliatis, usque ad circ. 2 cm. latis. Capitula pauca, corymbosa, subvalide pedunculata pedunculis superne pubescentibus circ. 4–8 cm. longis, demum circ. 2.5–3 cm. lata et 1.5–1.8 cm. alta; radio non viso. Involucri basaliter pubescentis bracteae exteriores circ. 7 vel 8, ovatae vel late lanceolatae, superne angustatae, apice obtusae, margine glabratae vel plus minusve ciliatae, tergo circ. 5–7-nerviae, 1.2–1.6 cm. longae et 3–6 mm. latae; interiores rigidae, oblongo-obovatae, tergo plus minusve hispidae, apice angustatae ac pubescentes, paulo breviores. Paleae lineares, apicaliter coloratae, achaeniorum aristas aequantes vel parce superantes. Achaenia plana, brunneo-atra, late vel moderate oblonga, unaquaque facierum circ. 16-sulcata, costis marginibusque creberrime papillata papillis setis munitis, corpore 7–8 mm. longis et 2–2.8 mm. latis, apice valde erecto-setosa et biaristata aristis subdivergentibus, rectis, apicem versus nudis inferne 1–3 hamis antrorsum hamosis, 1.5–2 mm. longis.

In a recent installment of their Flora of West Tropical Africa, HUTCHINSON and DALZIEL have described this new species, though in English and only in a scanty and preliminary way. They indicated the Kew Bulletin for 1931 apparently as the anticipated place

of a second and presumably more complete publication. The Kew Bulletin for 1931 appears, however, to lack any reference to the plant. Having made a study of some of the authors' original material and having found it referable more properly to *Bidens*, I am constrained to transfer the species to that genus. The name thus becomes **Bidens asperata** (Hutch. & Dalz.) comb. nov.

The first cited locality is Faranna, Sambadougou, French Guinea. *Aug. Chevalier* 20554, Cercle de Faranah (Faranna, Farana), "entre Sambadougou," Jan. 27, 1909 (Herb. Kew) has been studied by me and may be taken as the type.

CHICAGO NORMAL COLLEGE

[*Accepted for publication October 20, 1931*]

THE SUSPENSOR OF CRYPTOMERIA JAPONICA

JOHN T. BUCHHOLZ

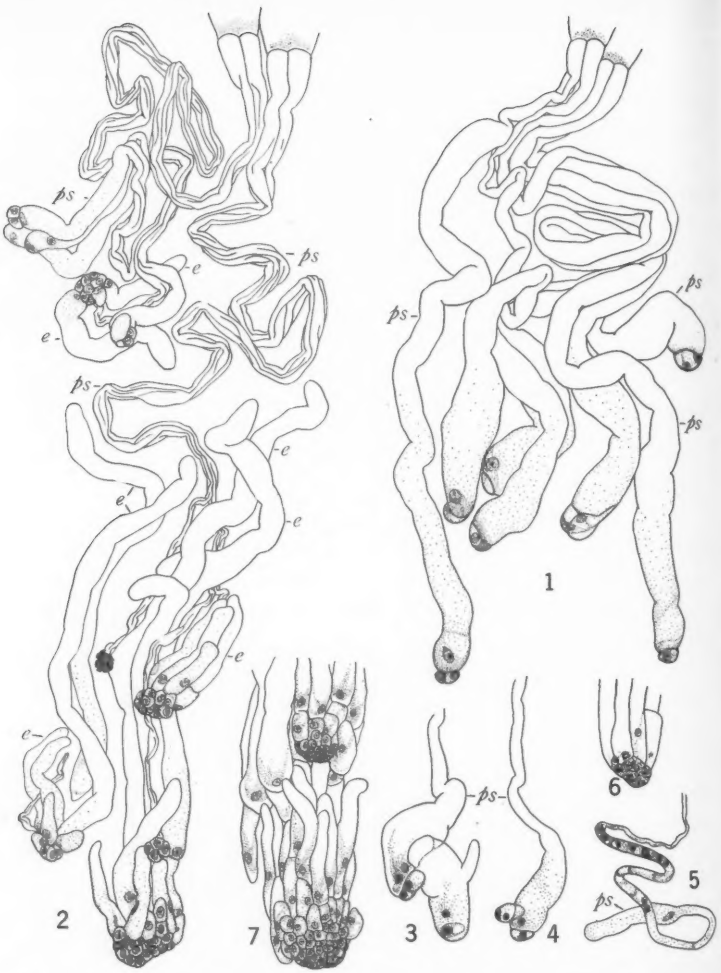
(WITH SEVEN FIGURES)

We owe our present knowledge of the morphology of *Cryptomeria japonica* to ARNOLDI (1) and LAWSON (5). MIYAKE (6, 7) has given us a similar account of *Cunninghamia*. These descriptions of the embryogeny are inadequate, however, in respect to the events following the first stage of suspensor elongation. LAWSON states, "there may be one or several embryos developed from a single archegonium." I cannot confirm this statement from observations, and there are several other important details of the embryogeny which justify further description.

In the summer of 1927, the writer investigated the embryo of *Cryptomeria*. The material was obtained on July 12 and 17 from trees growing at the New York Botanical Garden. The accompanying drawings show some of the stages which were dissected from the ovules.

As both ARNOLDI and LAWSON described them, the archegonia are terminal and grouped into an archegonial complex of about ten or twelve archegonia. This feature is common to most of the Taxodineae and Cupressineae. STRASBURGER (8) demonstrated that under these conditions both sperm nuclei of a pollen tube may function by being discharged into neighboring archegonia. A number of instances, including those illustrated in figures 1 and 2, showed two embryo systems coming from adjacent archegonia.

The proembryo has been described and figured as consisting of only two groups of cells and nuclei, arranged more or less in tiers, the uppermost tier consisting of free nuclei which soon disintegrate. The rosette tier usually found in the Abietineae, in *Cephalotaxus*, and frequently in *Sciadopitys* (3), is absent or may be considered as the uppermost tier which elongates to form the prosuspensor (*ps*). There are usually four or five elongating cells, which soon become separated into individual prosuspensor cells bearing the separated embryonic cells at their lower ends. All the cells of a proem-



FIGS. 1–7.—Fig. 1, two embryo systems of *Cryptomeria japonica*, in which elongated cells (*ps*) are separated strands of prosuspensors bearing embryo initials at tips. Some of embryo initials have divided, others are still single-celled, while a few prosuspensors without these cells at their tips have themselves become embryonic and cut off newly formed terminal cells. Fig. 2, two embryo systems in which many prosuspensor strands (*ps*) have become long and collapsed. Separate embryos are without unicellular primary suspensors, but the largest have formed a secondary suspensor of many long embryonal tubes (*e*). Figs. 3–5, lower portions and ends of individual prosuspensor cells which have become embryonic. Fig. 6, end of multicellular embryo on secondary suspensor as it appears in central plane of focus, showing apical cell and several segments. Fig. 7, surface view of largest embryo observed (this is probably near the oldest stage in which an apical cell may be identified); ×60.

bryo, whether they are embryonic cells at the tip or elongating cells, are potential embryo initials. This is shown by the fact that a prosuspensor cell, which breaks away from the group without bearing an embryo initial on its end, may become embryonic by cutting off a cell at its tip. These conditions are shown in some of the prosuspensors of the accompanying figures, where newly formed cells appear to be incorporated within their ends or are not so distinctly rounded off as the units found at the tip of the longest prosuspensor cell. In figure 2, the shorter embryo system above and at the left shows a newly formed cell at its end beside a neighboring prosuspensor cell which is still one-celled. As the prosuspensor cells elongate, the embryo initials at their ends usually become divided by a wall paralleling the long axis of the prosuspensor cell, as shown below at the left in figure 1. By the time the cells of the prosuspensor are fully elongated, the embryo units at the tip may be multicellular.

It is possible that occasionally two embryo initials may, for a time, be borne on a single prosuspensor cell; but there might easily be confusion here with a two-celled stage of a single embryo unit. If these are really two distinct embryo initials, they do not combine to form one embryo but develop independently. COKER (4) showed this condition in *Taxodium*. The largest embryo of figure 2 shows an instance in which a small independent group of cells is situated slightly above the larger one. Both of these cell groups seem to be associated with the same single prosuspensor strand which has now become completely collapsed. The smaller terminal embryo at the left in figure 2 has a torn prosuspensor end which may have been attached in a similar manner and broken off from the prosuspensor of the completely aborted embryo toward which its broken end is turned.

Cleavage polyembryony seems to be a characteristic feature of *Cryptomeria*. While only about 25 embryo systems were dissected, no exceptions were found in which the entire zygote produced a single embryo. Cleavage polyembryony is probably characteristic of the Taxodineae, since it is now known definitely for both *Taxodium* (4) and *Cryptomeria;* and it is probable that *Cunninghamia* (7), which is still incompletely known, may conform to this embryogeny.

Before some of the prosuspensor cells collapse, their lower ends may enlarge considerably. Sometimes they form balloons of con-

siderable size. If embryonic cells are cut off during this period of enlargement, the walls may be drawn out as flattened cells attached in curious shapes, and may become displaced on one side, while a new cell is cut off at the end. This is shown in the third embryo from the right in figure 1 and in other instances in the figures. Extreme examples of these conditions are illustrated in figures 3–5. Here the prosuspensor cells have cut off several embryonic cells. In figure 3 the enlarged end of a prosuspensor cell has cut off a terminal cell which has divided, and from one side it has produced a branch leading to another inflated portion, on the end of which a cell was cut off, which is now flattened out against the side at the back. In figure 4 a cell which was cut off and partially flattened against the side has grown out and cut off a small terminal embryonic cell, while the main part of this prosuspensor cell has cut off another terminal cell. In the prosuspensor cell (fig. 5) the long upper portion which is not all shown has collapsed. Below this is a region in which a row of seven or eight walled cells are found, while the slightly enlarged end contains several free nuclei. It is evident from these figures that prosuspensor cells may collapse completely if they become very long and have a large embryo attached. However, when they break loose, elongate less completely, or otherwise lose direct contact with an embryonic unit, they may become inflated in the lower end and cut off abnormal embryonic cells.

It is also evident from the different figures that prosuspensor cells usually become separated from one another and may develop in various ways. When vigorously growing embryos are developing at their tips, they tend to stretch out to a maximum length and collapse completely. When they are more retarded in their development, or are crowded back and cannot stretch to the maximum length, they may become inflated at the ends. If they lose their contact with an embryo unit, they may show their embryonic potentialities by internal cell proliferation or by cutting off embryonic cells near their ends, regardless of whether these ends are abnormally inflated or not. The embryos thus produced are not only retarded but are very abnormal in appearance; hence they probably do not contribute the successful embryo of the mature seed, which must first survive embryonic selection in competition with other embryos.

A little confusion might result from observation of an embryo such as the largest one in figure 2 if the collapsed prosuspensor strands were not observed. Such an error might easily be made from sectional material. The two or three longest embryonal tubes (*e*) might be mistaken for prosuspensors loosened and pulled out of the base of the egg, suggesting that possibly a single embryo might come from a union of all or nearly all parts of the zygote. It is obvious that an embryo may be derived from any cell in the proembryo, and that the separate embryonic units do not combine.

It appears that the embryo initial which has a chance of becoming the successful one is borne on a vigorously elongating prosuspensor cell, where it divides rapidly and becomes multicellular. Figure 2 shows several stages in which the more successful embryos have formed from ten to approximately fifty cells, and many of the cells adjacent to the prosuspensor have elongated as embryonal tubes to form a massive secondary suspensor.

The structure to which I have referred in previous publications as a primary suspensor (a single suspensor cell elongated singly from one of the individual lower embryo units) is not distinctly formed in *Cryptomeria*. There seems to be an abrupt transition from the prosuspensor cell which actually represents part of a different embryo to the massive secondary suspensor composed of many embryonal tubes. The embryonal tubes (*e*) may begin to elongate rapidly on several sides and surround the prosuspensor at about the same time, replacing the latter as it collapses.

In this development we may possibly find a fundamental difference between the Cupressineae (**2**), which also have cleavage polyembryony, and the Taxodineae as represented by *Cryptomeria* and *Taxodium* (**4**). The Cupressineae (*Biota* and *Libocedrus*) form prosuspensors which are not so long relatively, and the embryo initials which they carry forward form very long single-celled primary suspensors, before embryonal tubes begin to appear; while the Taxodineae form long prosuspensor cells and may suppress or entirely omit the primary suspensor. *Sciadopitys* (**3**) stands between these two extremes, in that both the prosuspensors and the primary suspensors become well developed.

Some evidence of apical cell growth was found in the individual

embryos. COKER's (4) figures of the early divisions in the embryo initials borne on the prosuspensor cells of *Taxodium* indicate that an apical cell stage may be identified in the earliest stages. Apical cell growth exists in the early stages shown here, but it is not always easily observed and cannot be shown to advantage in a drawing such as figure 7, which shows a surface view of cell arrangement. Figure 6 illustrates an embryo in a more central plane of focus, and shows the apical cell together with three of its segments to better advantage. From observations on the ends of certain embryos, the apical cell seems to have three cutting faces, and it appears that its period of duration may extend into as late a stage of the embryo as any which were observed in this investigation.

Summary

The outstanding features found in the embryogeny of *Cryptomeria* are cleavage polyembryony, the absence of typical primary suspensors, and the apical cell method of growth in the early embryo.

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[*Accepted for publication September 29, 1931*]

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ANOTHER HAPLOID NICOTIANA TABACUM PLANT

FRANCIS A. MCCRAY

(WITH FOUR FIGURES)

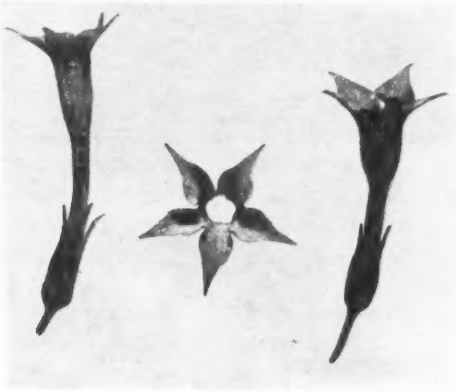
In the course of numerous tests of compatibility of *Nicotiana* species made in 1928, a quantity of seed was produced by using *glutinosa* pollen on *tabacum* var. *angustifolia*. This seed was planted in October, 1930. Good germination was secured but the seedlings were weak and made a very unsatisfactory growth. Because of this fact a larger number than usual were transferred from the germinating pan to individual pots. Altogether 18 plants were so tested, and all failed at the same early stage except one, which made a normal growth.

As this plant neared maturity it became apparent that it was a maternal, pure *tabacum* individual, thus explaining its success while the others, evidently hybrids, failed in development. Attracted first by the paucity of pollen in its flowers, the writer studied the plant both morphologically and cytologically. It soon became apparent that it was a haploid *tabacum*.

As in the case of the *purpurea* haploid described by CLAUSEN and MANN (3) and the merogonous *tabacum* haploid reported by CLAUSEN and LAMMERTS (2), this plant was an exact duplicate of the parent variety except that some size characters were reduced, which was especially noticeable in the flowers. The difference is shown in figure 1.

The typical distribution of the chromosomes in the pollen mother cell divisions in this haploid plant is shown in figure 2, which is taken to represent an attempted reduction division. No true metaphase plate is formed. A few chromosomes are clustered near the center of the cell, but most of them are scattered. The 24 chromosomes can be counted. This figure, which was drawn from an aceto-carmine smear, is closely similar to figure 5 of CLAUSEN and LAMMERTS. Figure 3 shows an unusual condition, a tri-polar spindle. In another

cell, illustrated in figure 4, drawn from a permanent preparation, there appears a nearly normal metaphase figure in side view, a phenomenon that appears only rarely. Only three chromosomes are off the plate. Still another cell shows the usual four groups of chromosomes at telophase. It was not possible to count accurately the chromosomes in any of these nuclei, but it is certain that the original chromosomes have divided. If both the divisions in this cell were mitotic, then it should be possible occasionally to get a functional gamete with a complete, or nearly complete, chromosome set.

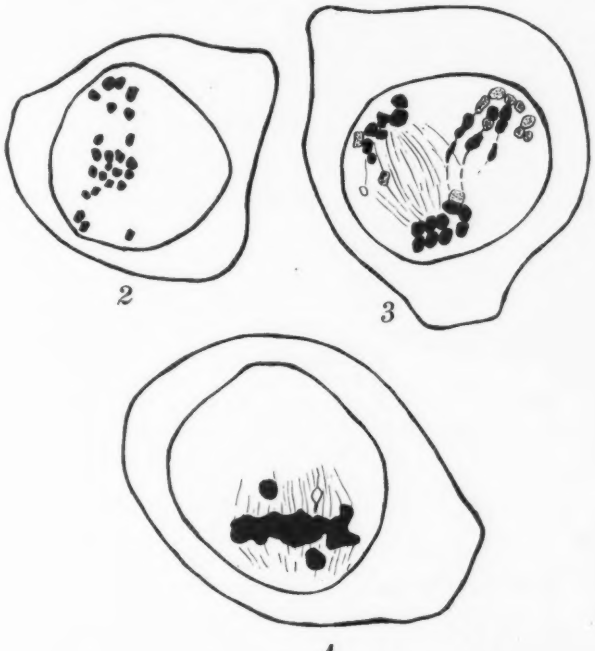


a *b* *c*

FIG. 1.—*a, b,* Flower of *Nicotiana tabacum* var. *angustifolia; c,* flower of haploid *N. tabacum* var. *angustifolia.*

CHIPMAN and GOODSPEED (1) were able to report some progeny from crossing the *purpurea* haploid with the *tabacum* parent, but all the flowers on my plant dropped whether they had been pollinated or not. It was pollinated four times by *tabacum* var. *sanguinea*, three times by var. *macrophylla*, four times by var. *purpurea*, twice by var. *angustifolia*, and also selfed five times. Pollen of the haploid was also used once on each of the *tabacum* varieties *sanguinea*, *purpurea*, and *macrophylla* without result. It is possible, of course, that if a sufficiently large number of trials had been made, functional gametes might have been discovered.

This haploid *tabacum* plant thus corresponds exactly in both morphology and cytology with those described in papers already mentioned. No doubt the diploid maternal, which appeared following a cross of *tabacum* var. *angustifolia*×*rustica* var. *pumila* and with which it is compared, had its origin as a haploid also. EAST (4) has



FIGS. 2–4.—Fig. 2, pollen mother cell in haploid *tabacum* plant: random distribution of 24 univalent chromosomes; drawn from an aceto-carmine smear. Fig. 3, pollen mother cell in haploid *tabacum* plant; tri-polar spindle. Fig. 4, pollen mother cell in haploid *tabacum* plant; side view of spindle resembling ordinary metaphase figure.

already emphasized the genetic possibilities of homozygous plants produced in this way. CLAUSEN and LAMMERTS, after finding their merogonous haploid *tabacum*, suggest that the *sylvestris*-like segregates from the backcross, (*sylvestris*×*tabacum*)×*sylvestris*, were probably merogonous diploids. Other pure segregates from hybrid

progenies may have had their origin in parthenogenesis or merogony, especially where the hybrids are only slightly fertile and only a few recombination types appear.

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[*Accepted for publication December 9, 1931*]

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CURRENT LITERATURE

BOOK REVIEWS

Families of flowering plants in northern China

The 127 families of flowering plants found in Hopei, "the nature of whose flora practically represents that of North China," are made the basis of a recent systematic treatise by LIU.[1] An analytical key for identifying plants of Hopei Province to the families or anomalous genera is given (pp. 41–53). "In addition, out of the total 632 genera met with in Hopei, analytical keys for 598 of them are given at the end of the family to which the genera belong." Thus the student should be able to identify all the plants of Hopei, and many of those in the adjacent provinces, not only to the families but "almost always to the genera as well."

Common Hopei plants are illustrated with 124 zinc engravings; these portray examples of all but six of the 127 families. Some 170 other figures, not to include several unnumbered pictures, illustrate mostly botanical terms used in taxonomy. It is interesting to note that "out of the total 294 figures included in this book, 278 are original and drawn from local plants, mostly in the fresh state." Many of the sketches are of plants known through cultivation or otherwise to American botanists and the originality displayed in the delineations will doubtless prove stimulating.

Various suggestions are given to students and collectors purposing to study the Chinese flora. Brief summaries of opinions upon plant classification are presented, but "the Bessey System is adopted in principle." The style is concise throughout. The text is primarily in English, although Chinese characters are used for Chinese equivalents. In numerous instances the grammar is faulty and the wording incompatible with idiomatic English. These imperfections will doubtless be removed in a subsequent edition. Meanwhile, however, the temptation to overlook them is strong because of the numerous points of excellence in other respects which LIU's very welcome volume displays.—E. E. SHERFF.

Introduction to agricultural biochemistry

This interesting book by DUTCHER and HALEY[2] will be of value to a large and growing number of biologists who find their work inevitably leading them into the field of biochemistry. It gives, in somewhat elementary fashion, a good

[1] LIU, J. C., Systematic botany of the flowering families in north China. pp. xxxiv+213. *Figs. 294.* Henri Vetch, The French Book Store. Peiping. 1931.

[2] DUTCHER, R. A., and HALEY, D. E., Introduction to agricultural biochemistry. 8 vo. pp. x+484. *Figs. 98.* John Wiley and Sons, New York. 1932. $4.50.

foundation for work in the agricultural field, and reflects the long experience of the authors as investigators and teachers in this subject.

The work is divided into three main parts. (I) A general introductory section of seven chapters, with titles as follows: development of agricultural chemistry; chemistry of living matter; carbohydrates; fats and related compounds; proteins; physical state of matter; and enzymes. (II) The plant. This section of thirteen chapters begins with seed germination, and continues with chapters on the soil; soil acidity; farm manure; fertilizers; the atmosphere; insecticides, fungicides and related materials; absorption of mineral nutrients by plants; assimilation of mineral nutrients by plants; plant carbohydrates; plant lipids; vegetable proteins and related compounds; and respiration. (III) The animal. This section is divided into twelve chapters, including such subjects as foods and feeding stuffs; digestion of foods; body tissues; metabolic changes in tissues; energy metabolism; biological response to foods; and protein quality. The last five of the twelve chapters treat of the vitamins A, B, (B and G complex), C, D, and E.

The book is clearly and simply written, holds the interest of the reader, and will no doubt stimulate many students to delve more deeply into the chemistry of the life processes of plants and animals. It will be a welcome addition to the literature for those taking the first steps in this fascinating field.—C. A. SHULL.

Zonation in colloidal media

The second edition of KÜSTER'S[3] work on zone formation in colloidal substances is an entirely new work, as it is nearly 20 years since the first edition (1913). The great diversity of the phenomena brought together leads one to question the value of the comparisons instituted. There are six chapters, the first of which deals with true Liesegang periodic precipitation phenomena in lifeless gels. The succeeding chapters discuss starch grains and other sphaerocrystalline structures, and lamellated membranes; vascular thickenings and pittings, lattice structures and marking of diatom shells; marking, spotting, and blotching of colors in petals of flowers and in seed coats, and ring-spot diseases of leaves; annual rings of trees, and zebrine markings of variegated leaves such as *Billbergia zebrina*, *Cryptanthus zonatus*, and *Aloe variegata;* and the "fairy ring" fungi. Any general principle which may bring into common consideration so many different phenomena, with so many different causal relations, is likely to be of little value, or too general to be very useful.—C. A. SHULL.

[3] KÜSTER, ERNST, Über Zonenbildung in kolloidalen Medien. 8vo. pp. x+124. Gustav Fischer. Jena. 1931. 8 RM.

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